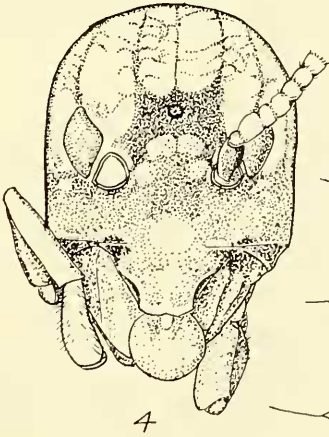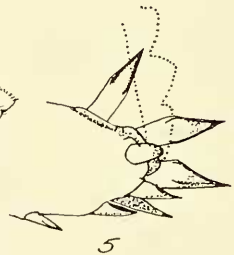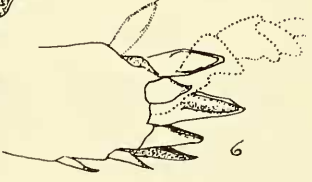del. E.R.Tinkham 1964

NOTES ON OTHER CALIFORNIA SPECIES

Stenopelmatus pictus Scudder.

A small, easily recognized species with dark piceous streaks, separated by narrow tan, sutural areas on the upper half of the head and with dark areas of shining black of irregular conformation on the dorsum of the pronotum. Scudder described this rather small species from San Francisco in 1897. Hebard (1916) added Palo Alto, and Davis and Smith (1926) added Suisun to its distribution. Two specimens before me, on loan from the Museum of Zoology, University of Michigan are: one female, Patterson Pass, Alameda County, California, and one male from Antioch, California, March 29, 1956, B. J. Adelson. I have a specimen from Stockton, California, April 15, 1960, collected by Jean Swagerty. It is evident from this brief information that the distribution, habitat, and habits of this interesting cricket are poorly understood at present.

Stenopelmatus longispina Brunner.

Originally described from Vancouver Island; Scudder (1899) added Ft. Boise, Drain, and Roseberg, Oregon, as well as several locations in coastal California to its range. Hebard (1916) indicated that *S. californicus* Brunner and *S. irregularis* Brunner were synonyms and gave a number of places as farther extending its distribution. *Stenopelmatus longispina* is a large reddish brown species characterized by the long, acuminate, conically tapering, internal calcar of the caudal tibia which is much longer than the other five. Much needs to be learned about the distribution, ecological niche, and habits of this interesting creature.

Stenopelmatus fuscus Haldeman.

This large reddish brown species Hebard recorded from many locations in the western United States, extending from Nebraska and New Mexico west to the Pacific Coast and from Montana south to Chihuahua, Mexico. Only a study of extensive collections from this vast area will decide whether there is only the one species or whether several geographic races occur. Hebard indicated that *S. cephalotes* Walker, *S. fasciatus* Thomas, *S. oculatus* Scudder, and *S. hydrocephalus* Brunner were synonyms.

Much still has to be learned about this large, handsome species which is distinguished from *S. longispina* by the more even character of the six calcars of the caudal tibiae, the inner faces of which are obliquely truncate and spatulate.

PROVISIONAL KEY TO KNOWN CALIFORNIA SPECIES

1. Size large; color of head and pronotum orange red 2
   Size medium to small; color of head and pronotum not orange red but piceous to shining black 3

2. Calcars of the caudal tibiae forming a semiringlet of six spurs, the two innermost much
       the longest and cylindrical in form .... *S. longispina* Brunner
    Calcars of the caudal tibiae forming a semiringlet of six, these spathulate or trowel-
       shaped on their inner faces, the three inner relatively equal and longer than the
       three outer spurs .... *S. fuscus* Haldeman
3. Entire body uniformly dark brown with black abdominal tergites. Caudal tibiae with
       four internal and two external dorsal teeth _____ *S. intermedius* Davis and Smith
    Upper half of head shining black with tan sutural areas; pronotum with dorsum bear-
       ing irregular areas of shining black. Femora marked with pale brown fasciations
       .... *S. pictus* Scudder

BIBLIOGRAPHY

DAVIS, ALONZO C., and LESLIE M. SMITH
    1926. Notes on the genus *Stenopelmatus* with description of a new species (*Orthoptera*).
       Pan-Pacific Entomologist, vol. 2, no. 4, pp. 174–181, 7 figs.

HEBARD, MORGAN
    1916. A study of the species of the genus *Stenopelmatus* found in the United States.
       Journal of the New York Entomological Society, vol. 24, no. 1, pp. 70–86,
       pl. 7.

SAUSSURE, HENRIDE, and ALPHONSE PICTET
    1897. [*Stenopelmatus* in their treatment of the family Locustidae.] Biologia Centralia
       Americana, Orthoptera, I, pp. 286–292, pl. 14, with 23 figs.

SCUDDER, SAMUEL H.
    1899. The Stenopelmatinae of the Pacific Coast. Canadian Entomologist, vol. 31, no.
       5, pp. 113–121.

STROHECKER, H. F.
    1945. Notes on and descriptions of Mexican Orthoptera. Annals of the Entomological
       Society of America, vol. 38, no. 2, pp. 207–215, 12 figs.

THE SYSTEMATICS OF THE PACIFIC TREE FROG, *HYLA REGILLA*

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The first review of the western forms of *Hyla* was by F. C. Test in 1898 in which he made some delightful comments on the use of poorly preserved specimens, "meager material collected at points whose precise location and geographical relation to each other were many times but vaguely understood" and "the too ready and free description" of new specimens. This could be taken as a condemnation of some of the practices of the last 65 years of the 19th century. The first 65 years of the 20th century have been characterized by more of the same, including some astounding statements by the senior author. Unfortunately the present work will not offer real solutions to the problem; in fact that is not our intention. If we can kindle the imagination, tease the doubters, and stimulate those who follow, we will have succeeded. We have collected more localities than Test had specimens (512), we have borrowed enough museum material to more than equal our own collections, and we have compared our animals with every North American hyla we could borrow and every hyla we could take the time to look at in our stay at the American Museum of Natural History in the fall of 1963.

With real hesitation we offer the following systematic consideration of a portion of the genus *Hyla* from western North America. The data are too meager, and we have been too ready and free in our descriptions. We would like to wait another 12 years, but we face the fact that, like it or not, this

must be done. We have genetic, physiological, and ecological studies which are short on, or completely lacking in, meaning, because the systematic analysis is not available to assist in their interpretation. We have the next round of studies to perform and these require the context of an attempted systematic treatment.

The senior author has long espoused the concept that a subspecies should be described only when to fail to do so would obscure more biological truths than would be lost by describing the subspecies. The reader should be warned that our subspecies is a biological one composed of morphological facts, ecological observations, physiological measurements, genetic approximations, and geological guesses. After reading the paper, some of our colleagues may insist that the subspecies have been drawn from random tables on a malfunctioning computer. Hamming (1962) has stated that "The function of computing is insight, not numbers." The discriminant analyses and factor analyses described here were used to gain information about similarities and differences rather than to establish statistical bases for conclusions. These methods are descriptive rather than statistical; the fact that statistical tests are available once computations are made is useful, but the fact that discontinuous variables in morphology, physiology, ecology, behavior, genetics, and development support the results is of more significance.

Nomenclatorial History

Hyla regilla was described by Baird and Girard (1852, p. 174) along with several other new species collected by the U. S. Exploring Expedition under the command of Capt. Charles Wilkes, USN. The description is based on "Specimens . . . collected on Sacramento River, in Oregon and Puget Sound." No type specimens were designated.

Yarrow (1882, pp. 171–172) listed a number of specimens of *Hyla regilla* in the U. S. National Museum (USNM), including no. 9182 collected by the C. P. Expedition from "Puget Sound, Alaska," but did not indicate which of these specimens, if any, he considered to be the types.

Cope (1889, pp. 360–363) listed a number of specimens of *Hyla regilla* in the U. S. National Museum, including the Puget Sound specimen listed by Yarrow, but also failed to indicate a type specimen.

Test (1898, pp. 490–491), in his list of *Hyla regilla* in the U. S. National Museum, includes two specimens collected by the C. P. Expedition: no. 9182 from "Puget Sound, Washington" and no. 15409 from "Sacramento River, California." Presumably Test believed that Baird and Girard's description of *Hyla regilla* was based on these specimens for he refers to both of them as type specimens of that species.

Schmidt (1953) restricted the type locality of *Hyla regilla* to Sacramento County, California, for the USNM 15409 and Fort Vancouver, Washington, for the USNM 9182. Cochran (1961, p. 58), in her list of type specimens in

the U. S. National Museum, lists the cotypes of *Hyla regilla* as 9182, Puget Sound, Washington, and 15409, Sacramento River, California.

Our examination of USNM 15409, now in very poor condition, indicates that it very probably represents an intergrade of various forms that conjoin in northeastern California. Several characters clearly show this—finger webbing is extensive, extending about one-third the length of the fingers, and ventral granulation appears to stop well before (2.5 mm.) the breast fold. Neither of these characters has been seen in specimens from the Sacramento area or for that matter in any of the *Hyla regilla* examined. At minimum, this specimen, USNM 15409, apparently was not collected in Sacramento County, California. USNM 9182, on the other hand, is in much better condition, and our examination of it indicates that it could very well have come from Fort Vancouver. For these reasons, and for several others, we here designate USNM 9182 as the holotype of *Hyla regilla,* and accept the type locality as Fort Vancouver, Washington, as designated by Schmidt (1953).

Hallowell (1852, p. 183) described *Hyla scapularis* from specimens obtained in Oregon Territory. In the same volume (1852, p. 301) Baird and Girard referred specimens collected by John L. Leconte in San Francisco to *Hyla regilla,* and placed *Hyla scapularis* in the synonymy of *Hyla regilla.* The type specimen of *Hyla scapularis* Academy of Natural Sciences of Philadelphia (ANSP) 1978 is in excellent condition. Unquestionably it may be referred to the race of *Hyla regilla* that now occurs in the vicinity of Vancouver. Thus, *Hyla scapularis* Hallowell is a synonym of the nominate race of *Hyla regilla.*

In 1854 (p. 96) Hallowell described *Hyla nebulosa* on the basis of specimens collected by Dr. Heerman at Tejon Pass (California). This description was immediately followed by a description of *Hyla scapularis* var. *hypochondriaca,* also based on specimens from Tejon Pass collected by Dr. Heerman. Both descriptions were republished in 1859 (pp. 21–22) with slight changes in punctuation and illustrations and the addition of two sentences under "Gen. Obs." following the description of *Hyla nebulosa.*

The specimens on which Hallowell based his description of *Hyla scapularis hypochondriaca* (USNM 3235 (9)) were listed under *Hyla regilla* by Yarrow (1882), Cope (1889), and Test (1898), and were designated as the cotypes of the form by Test. We have examined these specimens and concur with these authors that they may be referred to the race of *Hyla regilla* that occurs in the vicinity of Tejon Pass today.

A number of problems are involved in the identity of *Hyla nebulosa. Hyla scapularis* var. *hypochondriaca* is described (Hallowell, 1854 and 1859) to include the presence of "a narrow, dark colored vitta extending from the anterior margin of the eye to the snout, another much broader from the posterior margin of the eye to the shoulder; margin of upper jaw of same color as the vitta." The description of *Hyla nebulosa* does not mention vitta and includes "dark colored subcircular spots, about a line in diameter, scattered over the

upper part of the body, and upon the sides, . . . abdomen and under surface of extremities granulated, terminal disks much flattened"; and a detailed comparison with *Hyla versicolor*. Examination of the illustration of *Hyla nebulosa* shown in the redescription in 1859 (plate X) shows a specimen lacking the characteristic eye stripe and patterns of *Hyla regilla* and possessing the characteristic body form of the canyon toad. These drawings are reported to have been made in the field. The two sentences added to the 1859 description of *Hyla nebulosa* under "Gen. Obs." point out that *Hyla nebulosa* is similar to *Hyla delitescens*. Other authors have not recognized *H. delitescens*. The description by Le Conte (1825) and the description and illustration given by Holbrook would suggest *Hyla versicolor* or *Hyla phaeocrypta*.

We submit that the problem of *Hyla delitescens* is one to be solved by our eastern colleagues, but in any case the beast would be like the *Hyla californiae–arenicolor* group. The characteristics of *Hyla nebulosa* clearly distinguish it from the other species of *Hyla* currently recognized in the Tejon Pass region of southern California. Significantly, both the collectors and Hallowell recognized the existence of the two kinds of animals in southern California. Cope (1866) proposed *Hyla cadaverina* as a substitute name for the preoccupied *Hyla nebulosa*. Yarrow (1882) and Cochran (1961) list the type specimen of *Hyla cadaverina* as USNM 3230. Test (1889) lists USNM 3230 as the type of *Hyla cadaverina,* but this specimen is from Fort Vancouver, Washington. In the previous line Test lists USNM 3230 as the type of *Hyla nebulosa*. A typographical error in Test's paper appears evident. Cope (1889, p. 359) includes a description of the fresh type specimen of *Hyla nebulosa* (=*cadaverina*) and questions the validity of including this form in synonymy with *H. regilla*. The problem is further complicated by the obvious fact that specimen no. 3230 is not one of the animals referred to in Hallowell's original description, nor is it the specimen described by Cope in 1889 (p. 359); (table 1). At the end of his description Cope states "two specimens from Tejon Pass, southern California are located in the Museum Academy of Philadelphia." Hallowell's description refers to "both" specimens. The original cotypes of *Hyla nebulosa* (=*cadaverina*) appear to be lost in the general confusion. Thus, *Hyla nebulosa* Hallowell (=*Hyla cadaverina* Cope) is here considered to be a synonym of *Hyla californiae* Gorman, leaving *Hyla hypochondriaca* as the earliest available name for the race of *Hyla regilla* that occurs in the vicinity of Tejon Pass.

Cope (1866) described *Hyla curta* from 19 "half" adult specimens collected by Jno. Xantus at Cape San Lucas and catalogued under the number 5293. Yarrow (1882) lists these specimens as from Fort Tejon, California. The specimens are now accompanied by a label which indicates they were obtained on August 10, 1859 from Soria, 15 miles north of Cape San Lucas. They are small and faded, the eye mask is still present but the stripes are gone.

Cope (1889, p. 359) described *Hyla regilla laticeps* from eight adult specimens from Cape San Lucas, Baja California, compared it with *Hyla cadaverina,*

TABLE 1. *Comparative measurements taken on the holotype (USNM 3230) of* Hyla nebulosa *Hallowell (1852) (=* Hyla cadaverina *Cope (1866)) and the largest of eight syntypes of* Hyla scapularis hypochondriaca *Hallowell (USNM 3235).*

| | USNM 3230 | | | | USNM 3235 | |
	Hallowell (1852, 1854)	Cope (1889) Lines*	Inches	Jameson et al.	Hallowell (1852, 1854)	Jameson et al.
Snout–vent	$1\frac{7}{8}''$	19	$1\frac{7}{16}''$	$1\frac{3}{16}''$	$1\frac{1}{2}''$	$1\frac{9}{16}''$
Head width	$\frac{3}{4}''$			$\frac{3}{8}''$	$\frac{5}{8}''$	$\frac{1}{2}''$
Head length		5.9	$\frac{1}{2}''$	$\frac{3}{8}''$	$\frac{5}{8}''$	$\frac{1}{2}''$
Length anterior extremity	$1\frac{5}{8}''$			$1\frac{3}{4}''$	$\frac{7}{8}''$	$1\frac{5}{16}''$
Length posterior extremity	$2\frac{3}{8}''$	32.4+	$2\frac{3}{4}''$	$1\frac{29}{32}''$	$1\frac{7}{8}''$	$2\frac{3}{8}''$

* Twelve lines per inch.
+ By addition of femur, 8.7 lines; tibia, 10.6 lines; hind foot, 13.1 lines.

and suggested it was difficult to distinguish from *Hyla curta*. We concur with Cope and determine that the name available for the race of *Hyla regilla* from the Cape region is *Hyla regilla curta*.

Taylor (1938) described *Hyla wrightorum* from Springerville, Apache County, Arizona, and *Hyla cardenasi* from Puebla, Puebla, Mexico. K. P. Schmidt (1953) placed *Hyla wrightorum* in synonymy with *Hyla eximia*. We are of the opinion that this designation is in error. *Hyla lafrentzi* was described by Mertens and Wolterstorff (1929) from the Federal District, Mexico. *Hyla lafrentzi* was placed in synonymy with *Hyla gracilipes* by Kellogg (1932). Taylor (1938) considered *Hyla lafrentzi* a separate species and pointed out that the types of *Hyla gracilipes* differ from *Hyla eximia* by "differences so slight that I regard them as negligible," and he considered *Hyla gracilipes* Cope a synonym of *Hyla eximia* Baird.

We find that *Hyla wrightorum*, *Hyla lafrentzi*, *Hyla cardenasi*, and *Hyla regilla* from the northwest Pacific coast are practically indistinguishable; the differences are certainly much less than those distinguishing the other races of *Hyla regilla*. Therefore, we place *Hyla cardenasi* in synonymy with *Hyla lafrentzi* and we consider *Hyla lafrentzi* and *Hyla wrightorum* as races of *Hyla regilla*.

We are indebted to the following museums for the loan of specimens. (Each institution is designated by its abbreviation symbol): The American Museum of Natural History (AMNH), Stanford University Division of Systematic Biology (SU), University of California Museum of Vertebrate Zoology (UCMVZ), Chicago Natural History Museum (CNHM), the University of Texas Natural History Museum (UTNHM), University of Michigan Museum of Zoology (UMMZ), California Academy of Sciences (CAS), San Diego Museum of Natural History (SDMNH), and the San Diego State College (SDSC)

research collections. The SDSC research collections are transferred to the San
Diego Museum of Natural History on completion of each project.

METHODS

Measurements: Seventeen measurements representing various parts of the
animal were made on 149 randomly selected male animals of various (those
available) species of *Hyla.* The 149 male animals represented 19 species of
Hylidae. We were concerned at this stage with discovering the size and shape
differences and similarities of some currently recognized species of tree toads.
We intentionally did not include forms sometimes considered as different genera
(*Pseudacris, Acris*) and intentionally did include animals not necessarily closely
related to Pacific tree toads (*Hyla cinerea, H. gratiosa, H. loquax*). A discrimi-
nant function analysis was performed as described later. The per cent of sig-
nificant information obtained in each axis is given in table 2 along with the
characteristic roots of the discriminant functions. The coefficients of the dis-

Table 2. *Per cent of significant information and the characteristic roots (variance component) of the discriminant functions of 17 measurements and of 10 measurements of 149 male hylids.*

Number of characters measured	Axis	Variance component	Per cent total	Accumulated per cent
	1	1,956.54	46.9	46.9
	2	813.37	19.5	66.4
17	3	349.55	8.4	74.8
	4	260.32	6.2	81.0
	5	216.70	5.2	86.2
	1	1,945.44	64.9	64.9
	2	375.46	12.5	77.4
10	3	266.30	8.9	86.3
	4	140.36	4.7	91.0
	5	97.98	3.3	94.3

criminant functions were standardized by their respective variances. From these standardized coefficients and from a consideration of the cost, time, and accuracy of the measurements, we were able to reduce the number of measurements. We were interested in measurements which contributed the most to the discrimination of the animals into groups; therefore, we selected from those measurements with large standardized coefficients. We were also impressed by the fact that the shape and form of Pacific tree toads from various localities were different and we were concerned with measuring the size and shape variation in the animals. As a primary indicator of size we selected snout–vent. Appendage lengths are represented by shank length, forearm length, and length of fourth finger. Head length is shown as a total measurement and as partitioned into an anterior estimate of the length of the face (eye to nostril) and a posterior estimate of the length of the cranium (tympanum to eye). Face height is represented by the nostril-to-lip measurement. The difficulty of measuring cranial height and obtaining results forced us to abandon this measurement; this is compensated by the apparent correlation between cranial width, height, and length. An estimate of the area of the toe pad is obtained by measuring the width of the toe pad. We then reanalyzed the 149 male animals using only these 10 measurements, and found that we had gained in our ability to discriminate between systematic units of related and currently accepted tree frogs. We plotted the sample means from both the 17-measurement analysis and the 10-measurement analysis, and found that the distribution of the samples on the first and second principal discriminant axes was very similar. With 17 measurements we are able to obtain only 47 per cent of the information in the first principal discriminant axis while with only 10 measurements we are able to obtain 65 per cent of the information in the first principal discriminant axis. The total
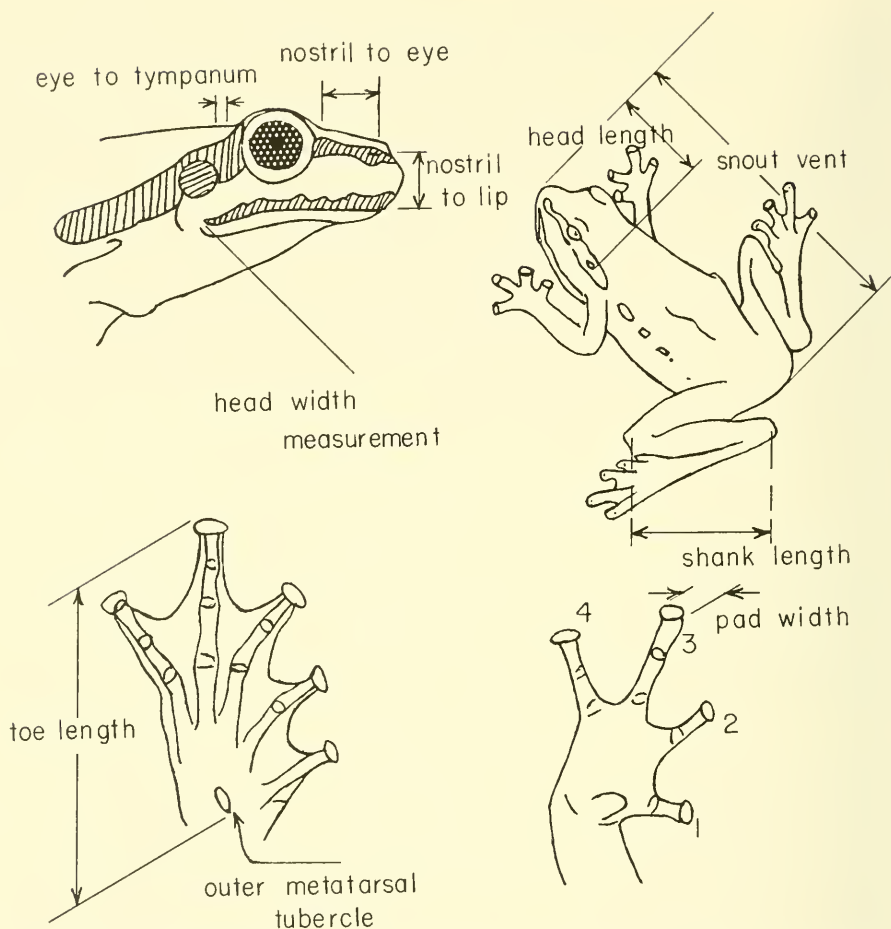
Figure 1. Measurements used in the analysis of size and shape variation within and between the subspecies of *Hyla regilla*.

variance (represented by the sum of the eigenvalues) for the 17 measurements is 4,160 and that for 10 measurements is 3,020; the variance in the first five axes is 3,596 (87%) and 2,825 (94%) for 17 and 10 measurements, respectively. Thus we lose about 25 per cent of our information by discarding seven measurements, but we greatly increase our ability to use (that is, reduce to a single discriminant function) the measurements we retain. We have significantly reduced our cost of measuring by more than half and our cost in computer time by more than two-thirds. We have used computer programs which are available in most installations to predict the usefulness of measurements and to estimate the cost of the study. This is a procedure we highly recommend. The

10 measurements (fig. 1) were obtained as follows: The first four measurements were taken with the aid of a dissecting microscope. The nostril–lip measurement was made perpendicularly from the ventral edge of the nostril to the upper lip, the eye–nostril measurement was made from the anterior edge of the eye to the posterior edge of the nostril, the tympanum–eye measurement was made from the anterior edge of the tympanum to the posterior edge of the eye. Pad width was measured on the third digit at the widest part of the pad. The remainder of the measurements were taken with a pair of vernier calipers (Helios-Braun Chemical Company). Head length was measured from the posterior edge of the tympanum to the end of the snout. Head width was measured at the angle of the jaw. Snout–vent length was from the end of the snout to the anus. Shank length was taken as the length of the left tibio–fibula. The forearm was measured by bending the hand backwards and placing one of the caliper arms on the palm and the other on the elbow. The length of the fourth toe was measured from the posterior edge of the outer metatarsal tubercle to the tip of the fourth toe. Measurements made in 1957 by one of us (J.P.M.) on the Oregon animals were found useful for separate analysis as were measurements made in a different study by G. Schroeder in 1960 and T. Vogt in 1961, 1962, and 1963. With these measurements we were able to test some of our conclusions. We also tested the possibility of grouping measurements made by more than one investigator and found the procedure unsatisfactory. Slight differences in measurements of the same animals (samples) by different investigtaors are (1) not describable in terms of this section, (2) not significantly different in terms of univariant statistics (T tests), and (3) significantly different in terms of multivariate statistics.

The use of discontinuous variables in amphibian studies is plagued by the lack of discrete things to count or identify as clearly present or absent. Many discontinuous variables are actually polygenic characteristics which have passed some threshold. The most useful approach has appeared to be to make some attempt to quantitize continuous variables. Test (1898) considered in detail the colors and stripes of the museum specimens he had at his disposal. He distinguished five categories ranging from little to much pigmentation and concluded (p. 486) "the different styles are so closely connected, and to a great extent actually confluent, that the unity as a species in this respect is very evident." We have studied the development of these patterns and colors and have found that they have geographic variability and that this geographic variability has interest and probably some evolutionary significance, but in terms of museum specimens there are severe limitations to their usefulness. They are subject to seasonal, age, health, background, light, temperature, and excitement modifications. The information given here on color is selected to be useful (in terms of identification of individuals and recognition of systematic groups) rather than comprehensive. A preliminary report on this is available (Resnick

and Jameson, 1963) and more comprehensive reports are in progress. The use of characteristics such as amount of wedding, granulation, pigment, and position and shape of teeth and other characters is justified on the basis of tradition and —more practically—they work. While we are certainly convinced that animals from different localities can be distinguished by differences in body form and shape, these are almost impossible to describe convincingly. For this reason we have turned to factor analysis and have found it expressive.

Mathematical Analysis

Now that we have reduced the number of measurements to 10, we are still faced with the complex task of looking at each set of measurements with respect to each other set of measurements for each of the samples available. To associate one variable with another by the usual bivariate graph would require 45 separate graphs, each with as many groups of data as there are samples. Multivariate discriminant analysis is useful since many characteristics and groups can be considered simultaneously, and an estimate of the amount of the total variation in each discriminant function is available. Further, we have statistical tests to tell us when we have considered the available, significant information with some predetermined degree of accuracy.

Multivariate procedures require that the data be normally distributed, or that normality be obtained by some transformation; in general, the requirement for normality extends to both bivariate and multivariate perspectives. Most metrical biological data is normally distributed or the data is so obviously not normally distributed that the decision is not a problem. In any case reasonable tests are available and were used.

There are a number of relatively straightforward expositions of multivariate procedures available. Cooley and Lohnes (1962) have the advantage of being comprehensive without being overly abstract and have the additional advantage of providing both computation procedures and some examples. The most concise statement we have found is that of Jolicoeur (1959), and we particularly recommend pages 287 and 298 of his paper; this work is additionally useful because it is a study of geographic variation. The two procedures we have used are (1) multivariate discriminant analysis and (2) factor analysis.

Multivariate discriminant analysis: Imagine a universe with 10 separate planes passing through a single point. The 10 planes represent our 10 measurements (X_i; $i = 1$–10). The point is the mean of each measurement. Within this 10-dimensional universe the mean of each sample (population, subspecies, etc.) is plotted with respect to each of the 10 characters. If one now shines a light through this array the position of each population casts a shadow on a screen held opposite the light. We have in effect created a marginal distribution which represents our discriminant function. We can rotate the light and screen in such a way as to maximize the between-group (B) variation and

to minimize the within-group (W) variation. Naturally, we have not described all the variation in this one plane (marginal distribution, discriminant function), but we can eliminate (algebraically) the variation we have described and repeat the process to find the marginal distribution (plane) which maximizes B and minimizes W of the remaining variation. The process is repeated until all the variation is accounted for. For each plane there are coefficients (K) of the discriminant function such that $K_1X_1 + K_2X_2 + K_3X_3 + \ldots K_{10}X_{10} = P$ which is the point on the plane represented by the animal with the measurements $X_1 \ldots X_{10}$. The use of the sample means ($\bar{X}_i$) will allow us to plot the means of each population. These coefficients (K) are direction cosines and the sum of their squares total 1.00; that is, they total to all the contribution of the measurements to the position of each animal or sample in plane under study. Because we successively account for all the variability, we also note that the sum of the squares of all the K_1's totals to all the contribution of the measurement X_1 to all the discriminant functions. In this way we are able to determine the contribution of a given measurement (X) to the discriminant function by the size of its coefficient (K). Each discriminant axis has a characteristic root (variance component, D) and the sum of these roots can be used to make tests of the significance of the information in the discriminant functions. The ratio of the size of the characteristic root to the sum of all the roots is an estimate of the per cent of the information (variation) described by that discriminant function.

The dispersion of the group means around their grand mean is expressed by the between-group covariance matrix B. The within group variance–covariance matrix W is the set of individual mean squared deviations and cross products. The standardization of matrix B by matrix W ($B \times W^{-1}$) accomplishes two things: (1) it adjusts each measurement by the variance of every other measurement and thus allows the emphasis of factors other than age or size in the determination of the differences between samples; and (2) it allows us to algebraically maximize the between-group variance and at the same time minimize the within-group variation.

At this point we are able to plot two discriminant axes at once (fig. 2), showing the per cent of the variation in each axis, the position of each sample mean, and of the grand mean on each axis. Additionally we can plot the co-ordinate axes of the original measurements as shown by the arrows emanating from the grand mean on each of our discriminant figures. The length of each vector (arrow) is determined by its variance. We have shown one or two standard deviations depending on visual requirements of the illustrations. The vector shows how the grand mean (and thus the discriminant function) would be changed if the measurement represented by that vector was allowed to vary independently.

FACTOR ANALYSIS. This consists of a detailed analysis of the within-group
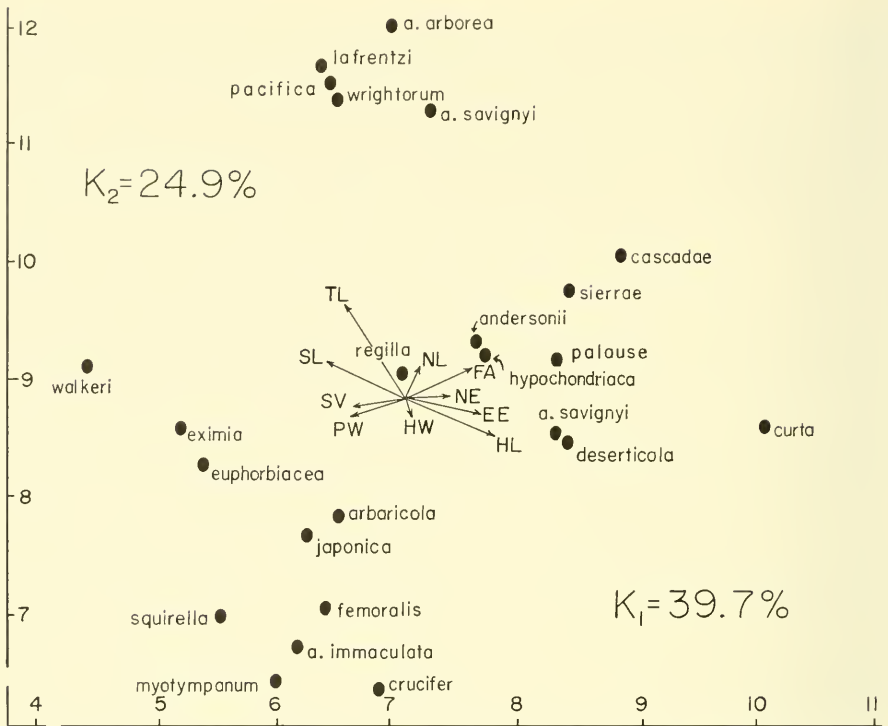
FIGURE 2. Discriminant analysis of 149 male hylids representing various recognized species and subspecies. The mean of each sample is shown on the first ($K_1 = 39.7\%$) and second ($K_2 = 24.9\%$) discriminant axes. The original coordinates are represented by the direction of each vector emanating from the grand mean. The length of the vector is representative of one standard deviation of the measurement. The measurements are labeled as indicated in table 5.

variation (W). A number of methods have been used and are described in Harmon (1960). We used both Hotelling's principal component and the Jacobian method, depending on accuracy and speed of computation required. Consider for a moment a single sample of animals and the 10 measurements plotted on the 10 dimensions of our universe. If we again make use of the light and screen we will find that the points of our sample of animals can be circumscribed by a multidimensional equal-frequency ellipsoid, the principal axis of which is parallel to our screen when we have maximized the variation of the sample about its mean. This principal axis is algebraically obtained from the variance–covariance matrix (W) or the correlation matrix (R) in the same way the discriminant function was obtained from the standardized B matrix. Characteristic roots (D) and coefficients (K) of characteristic vectors (principal component axes) are obtainable and they have comparable characteristics to

those described for the discriminant function. In this case we are examining the samples with respect to the principle trends of variation within the sample and we find that the first axis will be essentially a size component. Other axes will represent shape components, and the contribution of the original measurements to these components is discernible by the magnitude of the coefficients (K) since the sum of the squares of the coefficients represents all the variation. Factor analysis is used here to describe systematic units. Its use to determine parameters of growth (see Jolicoeur, 1963) in these frogs will be presented elsewhere.

The roots of the correlation matrix provide a factor solution to the question, "How many unique reference axes are required to explain the variation present in the 10 measurements." Harman (1960, p. 363) has recommended (following Kaiser) the use of those roots greater than 1.0. No more than two roots are greater than 1.0 in any of the subspecific groups we have analyzed here, and we have provided the direction cosines derived from the first two roots with respect to each of the measurements.

A number of rotational schemes are available. One of these (Quartimax) seeks to maximize or at least to emphasize the variation of the measurements; the object in our case would be to provide each measurement with a large direction cosine coefficient on only one or at least a very few factors. This would, in effect, give the amount of adjustment by each other measurement required to explain the variable under consideration. Another solution (Varimax) is to simplify the factors; the result is to rotate the axis so that the smallest number of measurements is responsible for each factor. Both the Quartimax and the Varimax solution are orthogonal. An oblique solution which provides properties of both rotational schemes is also available. For the present study we utilize the unrotated direction cosine matrix because we wish to emphasize the correlations present in the animals.

Selection of specimens and the use of a computer to search: The distribution and abundance of organisms as illustrated by museum collections has a number of built-in biases which prevent or at least make meaningless the use of random techniques. We have made the following assumptions.

(1) Collectors went where they thought the animals would be found.
(2) Collectors tend to collect the rare animal more than the common ones, but large samples are less subject to the error of the intentional collection of a single unusual individual than are small samples.
(3) Detailed maps of distribution based on museum collections tend to show where the collectors have been rather than where the animals are to be found. For this reason we have not attempted to locate every animal in every collection and we have not attempted to map every animal in every collection. We believe that this would be detrimental to the advancement of our understanding of the knowledge of the beasts because it would tend to obscure the problems that need to be solved.

We are providing classical distribution maps, but the type of maps we believe will be most useful are being prepared as parts of other studies.

(4) Rather than attempt to rule out by artificial means the opinions we have developed during the past 12 years about the various kinds of tree toads that may exist, we have attempted to capitalize on and test these opinions. As one of our colleagues has expressed of his own systematic work, "I find in nature what I believe to be a species, then attempt to find the morphological basis for this belief."

(5) A large number of measurements on one animal is better than one measure on a large number of animals.

(6) We cannot possibly measure all the frogs available and poorly preserved animals are generally not worth measuring.

The procedure may be summarized as follows:

I. (1) We selected localities represented by large samples (10 or more animals). (2) We selected localities from many different parts of the range including as parts: states, river drainage patterns, mountain ranges, physiographic provinces, biotic communities, and vacant spots on a map after the above localities were mapped. (3) We selected at least 10 different adult male animals from each locality. (4) We performed a discriminant analysis and plotted the $K_1 K_2$ and the $K_3 K_4$ and sometimes the $K_5 K_6$ axes to see which of these samples was similar morphologically and was contiguous geographically, topologically, or ecologically. (5) From this analysis we made predictions about where we would expect to find samples which were like the samples we had already measured and where we would expect to find samples which were intermediate between samples we had in hand. (6) We searched the collections we had on hand for samples meeting criteria in (5).

II. We repeated 3, 4, 5, and 6 until we had (a) run out of specimens from critical localities or (b) had obtained the same results over and over so that further expenditure of computer time would not appear to be justified.

III. We performed factor analysis on (a) all the animals measured to this point and (b) each group of presumptive races of animals we had in hand. The analysis of each group did in fact show us one locality which we had placed in the "wrong" group and that we had missed the significance of this placement when we had studied the discriminant plots. The displaced locality also showed us the power and significance of the factor analysis; nothing we read and nothing we tried was so convincingly instructional as this mistake.

IV. We then analyzed the groups we had identified on the basis of similarities in size and shape for discontinuous characteristics which would in fact allow us to accept them as systematic categories.

V. Throughout the process we were confronted with cases where previously unexplainable observations were now apparent. Again and again we would review the analysis and see things we had not noticed before; these observations led us back to the animals, field notes, and laboratory experiments where we found confirmation of our results.

We must emphasize that we also found items which do not make sense, and we found items which were in contradiction to all other observations. We even found on one occasion that rarest of events—a computer error so small that it could have been missed. In fact, we would probably miss it today, but at that time we were skeptical of every number.

Again may we emphasize that we used the computer as a tool to search and to discover, not as an end itself. The computer is one more tool to go along with the microscope, the calipers, the typewriter, the sonograph, the slide rule, and the meter stick. The mathematical analysis is one more piece of information to go along with snout-vent length, number of spots, color, temperature, odor of the water, slope of the land, number of people, and our concepts of evolution.

RESULTS

The preliminary analysis of the 149 animals by both the original 17 and by the extensively used 10 measurements (fig. 2) led us to the following conclusions about the size and shape of these frogs: (1) Several forms are so constructed that whatever relation they have to the frogs we are interested in must be found in characteristics other than size and shape. (2) Much the same body form is found in *Hyla eximia*, *H. euphorbiacea*, and *H. walkeri* and these species can be distinguished from *Hyla squirella*, *H. femoralis*, and *H. crucifer* which are similar to each other. (3) The Old World *Hyla arborea* can be separated into two morphological groups with respect to size and shape. (4) We were able to recognize the similarity of the body form of *Hyla regilla*, *H. lafrentzi*, and *H. wrightorum* and to recognize certain differences between them and the *H. eximia* and *H. squirella* "body form group" listed above.

The first discriminant analysis following the procedure outlined in step I above consisted of 41 samples of *Hyla regilla–lafrentzi–wrightorum*. The plots of the sample means suggested that the *H. regilla* populations concentrated in the coastal regions of Oregon, Washington, southern British Columbia, and northern California (fig. 3D) and those recognized as *H. wrightorum* (fig. 3J) from the Great Basin and Arizona and *H. lafrentzi* (fig. 3I) from central Mexico constituted a similar but separate group from all other regillas. Other groupings which appeared justified were the animals from (1) the coast range mountains of California and northern Baja California, (2) high elevations within the Sierras, (3) high elevations within the Cascade Mountains,
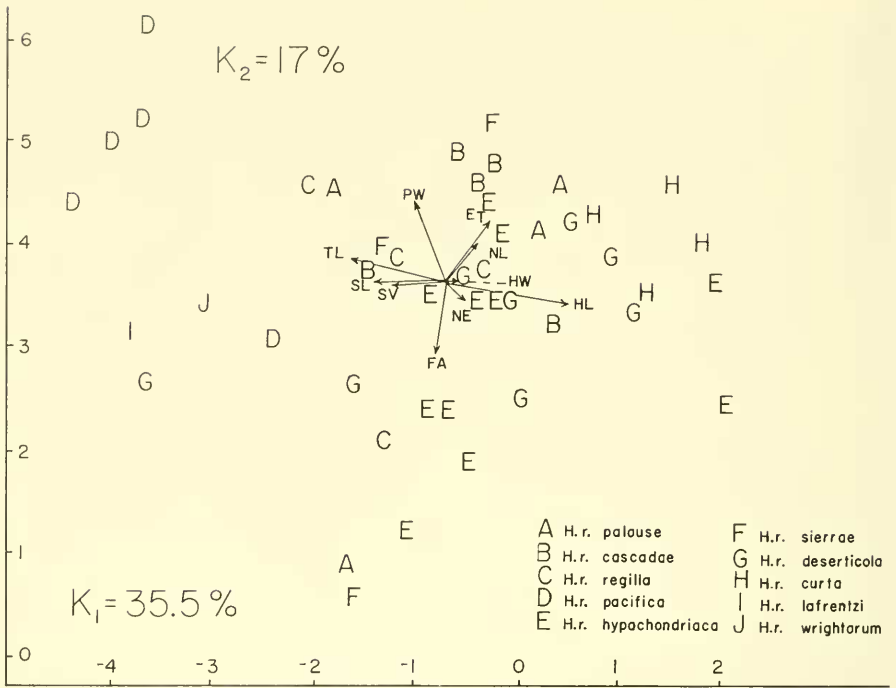
FIGURE 3. Discriminant analysis of 41 samples of *Hyla regilla* from various localities in western North America. The mean of each sample is shown on the first ($K_1 = 35.5\%$) and second ($K_2 = 17\%$) discriminant axes. The symbols are those shown on the map (fig. 11). The original coordinates are represented by the direction of each vector emanating from the grand mean. The length of the vector is representative of one standard deviation of the measurement. The measurements are labeled as indicated in table 5.

(4) the Cape region of Baja California, and (5) isolated desert populations in California, Baja California, and Nevada. Procedure II as given in Methods confirmed the outcome of the previous analysis. We then removed the northwest coastal *H. regilla–wrightorum–lafrentzi* samples and concentrated on the analysis of the remaining populations. Procedure II was repeated. The Puget Sound region and the Willamette Valley form a similar ecological habitat, and animals (and plants, Detling, 1948) from these regions are similar. The animals of the coastal regions of California are very similar to each other, but the analysis at this step left uncertain how far inland this group exists. The Sierra Nevada and the Cascade Mountain animals appeared to be similar to each other and to those from the foothills of the Rockies in Idaho and Montana. The grouping of isolated desert populations, northern Baja California populations, and inland California populations was in doubt. Specific areas were approached dealing with more or less local and discrete problems. Soon we
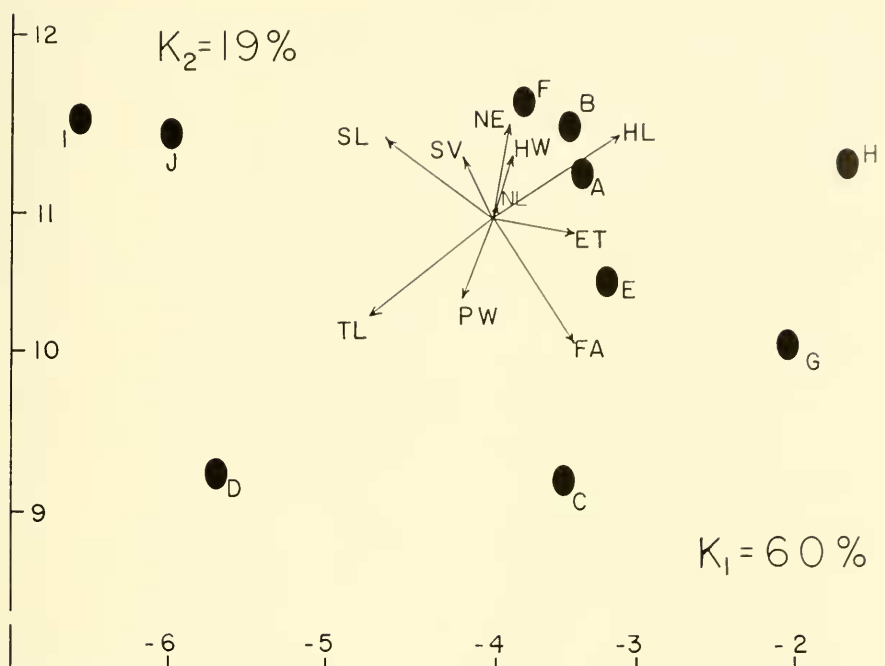
FIGURE 4. Discriminant analysis of the males of the 10 subspecies of *Hyla regilla* recognized in this study (table 3). The mean of each subspecies is shown in the first ($K_1 = 60\%$) and second ($K_2 = 19\%$) discriminant axes. The original coordinates are represented by the direction of each vector emanating from the grand mean. The length of the vector is representative of one standard deviation of the measurement. The measurements are labeled as indicated in table 5.

reached saturation and either ran out of animals or of new information. We then grouped the samples and computed a discriminate analysis on the "presumptive races" giving the results of figures 4, 5, and 6 and table 3.

DISCRIMINATORY ANALYSIS.

The partitioning of the latent roots of the discriminant matrix of 10 measurements of 454 males of *Hyla regilla* when they were grouped into 10 subspecies is shown in table 3. The total variance is 1,712.6, which is highly significant. The amount of variance in the first discriminant function is 1,033.9, which is 60.1 per cent of the total. The second discriminant function has a variance of 328.9 which is 19 per cent of the total. The first two axes have 79 per cent of the total variance of the 10 measurements, and they were plotted in figure 4. The smaller relative shank length and toe length of *H. pacifica* (D). *H. lafrentzi* (I), and *H. wrightorum* (J) set them aside as a separate group. The increased length of the face and head are characteristic of the relation of *H.*

TABLE 3. *Discriminatory analysis of 10 measurements of 454 males of* Hyla regilla *grouped into subspecies. The probability indicates the significance of losing information if that axis and all smaller axes are discarded from the analysis. Only those axes with* P *values smaller than 0.05 are given.*

Discriminant axis	Variance component	Per cent of total	Degrees of freedom	Proba- bility
1	1,033.9	60.3	18	<0.01
2	328.9	19.2	16	<0.01
3	122.9	7.2	14	<0.01
4	79.7	4.7	12	<0.01
5	68.4	4.0	10	<0.01
6	52.8	3.1	8	<0.01
7	19.7	1.2	6	<0.01

FIGURE 5. The mean of the male samples of each subspecies is shown on the third (K_3 = 7%) and fourth (K_4 = 4.6%) discriminant axes (table 3). Symbol and vector labels are as in figure 4.
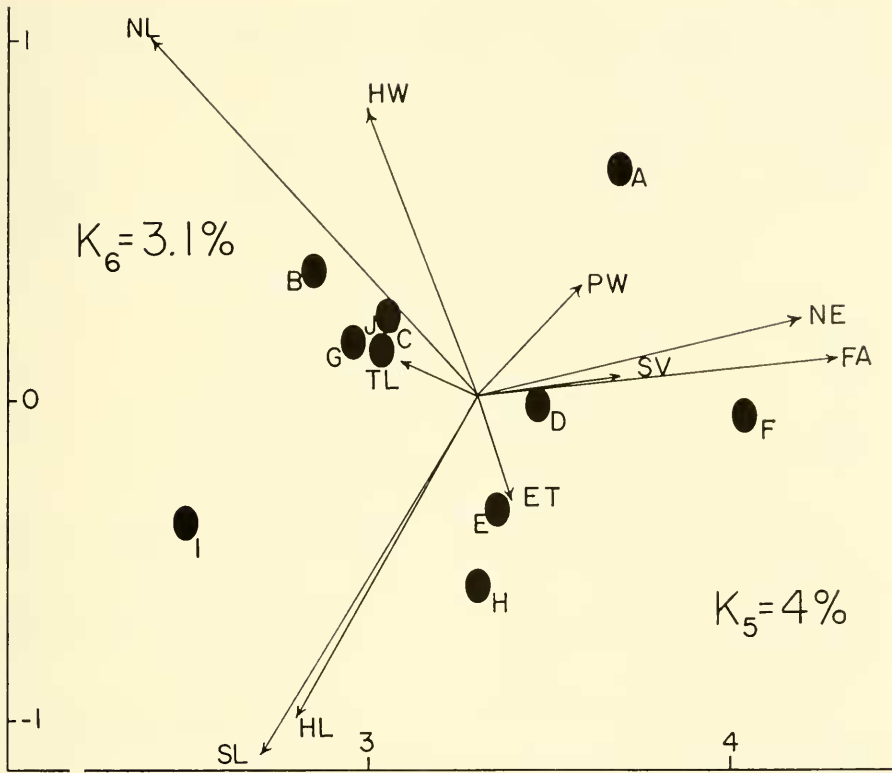
FIGURE 6. The mean of the male samples of each subspecies is shown on the fifth (K_5 = 4%) and sixth (K_6 = 3.1%) discriminant axes (table 3). Symbol and vector labels are as in figure 4.

r. sierra (F), *H. r. cascadae* (B), and *H. r. palouse* (A) to each other and the forearm length and eye–tympanum length indicate their relation to *H. r. hypo-chondriaca* (E) and *H. regilla* (C). Increase in the relative appendage lengths, eye–tympanum length, and face length distinguish *H. r. curta* (H) and *H. r. deserticola* (G) from other forms.

The plots of the third (variance 122.9, 7.2 per cent) and fourth axes (variance 79.7, 4.7 per cent) indicate the relatively longer snout–vent length in *H. wrightorum* (J), and demonstrate some of the proportions by which *H. r. pacifica* (D) and *H. lajrentzi* (I) differ from *H. wrightorum*. Comparison of the plots of the first four axes with that of the fifth (variance 68.4, 4 per cent) and the sixth axes (variance 52.8, 3.1 per cent) indicates the usefulness of the length of the vectors (determined by their standard deviation) in determining the magnitude and significance of the differences between the groups. Obviously the differences indicated by the plots of the axes with the smaller

TABLE 4. *Discriminatory analysis of 10 measurements of 90 females of* Hyla regilla *grouped into subspecies. The probability indicates the significance of losing information if that axis and all smaller axes are discarded from the analysis. Only those axes with* P *values smaller than 0.05 are given.*

Discriminant axis	Variance component	Per cent of total	Degrees of freedom	Proba- bility
1	495.1	60.9	18	<0.01
2	144.4	17.7	16	<0.01
3	84.8	10.3	14	<0.01
4	53.8	6.6	12	<0.01
5	17.3	2.1	10	<0.01
6	7.9	0.4	8	<0.05

variances have considerably less significance than those indicated by the plots of the first two axes and particularly of the plot of the first axis where 60 per cent of the variance is found.

The available females were separated into the same groups as the males, and a discriminant analysis was performed (figs. 7 and 8; table 4). The groupings and the differences between the groupings in the females are very similar to those indicated in the males. The toe is longer in *H. r. pacifica* (D) than in the others, *H. r. curta* (H) has a longer head, and *H. lafrentzi* (I) is distinguished by its shank length and nostril–lip measurement.

The first two discriminant axes of the males and the females considered at the same time are shown in figure 9. The diagonal separation of the males from the females suggests that the sexes can be distinguished in shape and form by the use of some function of a complex variable which we have not attempted to derive.

FACTOR ANALYSIS OF SIZE AND SHAPE VARIATION.

The use of the correlation matrix (R) to obtain the latent roots and direction cosines (matrix U) allows us to examine the principal sources of variation in size and shape in our animals. The first principal component axis should be essentially a size component. If all parts grow at equal rates (isometry) the coefficients of the direction cosines (U_{1i}) of each of the 10 measurements ($i = 1, 10$) should be $\sqrt{1/10} = 0.316$ because the expected value of the direction cosines is $\sqrt{1/P}$ where P is the number of measurements. The magnitude of the deviation from isometry (i.e., $0°$) can be calculated by $\cos \phi = U_1 V_1 + U_2 V_2 + \ldots U_{10} V_{10}$ where: $v_i =$ isometric value of 0.316, $u_i =$ observed direction cosine value.

The other axes should represent shape variation in the animals studied. The number of principal component axes preserved for study may be estimated by the Kaiser rule of the thumb (roots larger than 1 accepted), by the per cent of information given by that root and by testing roots to determine if one
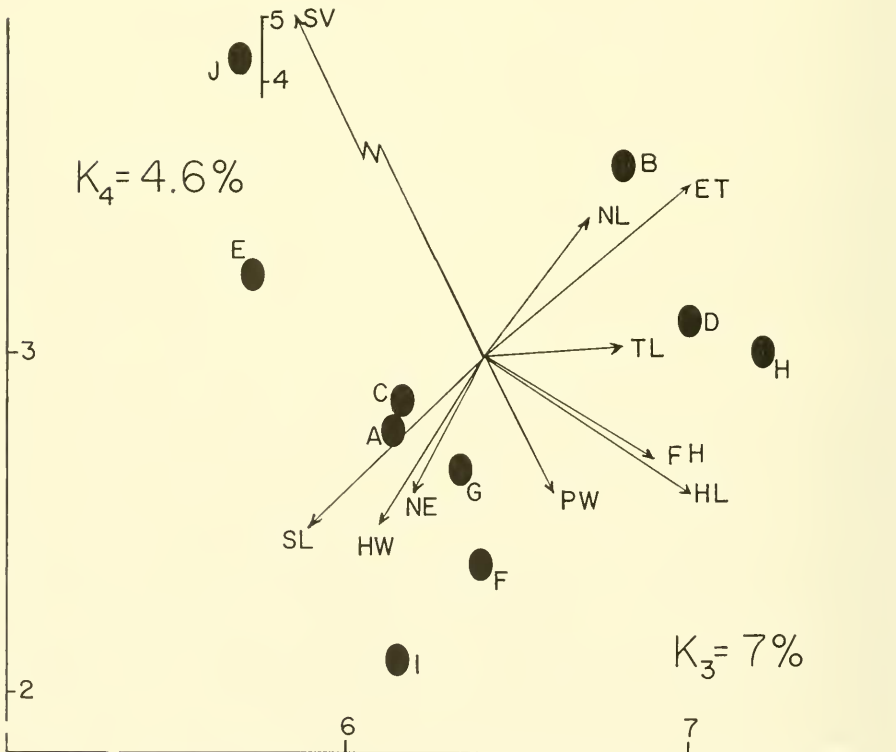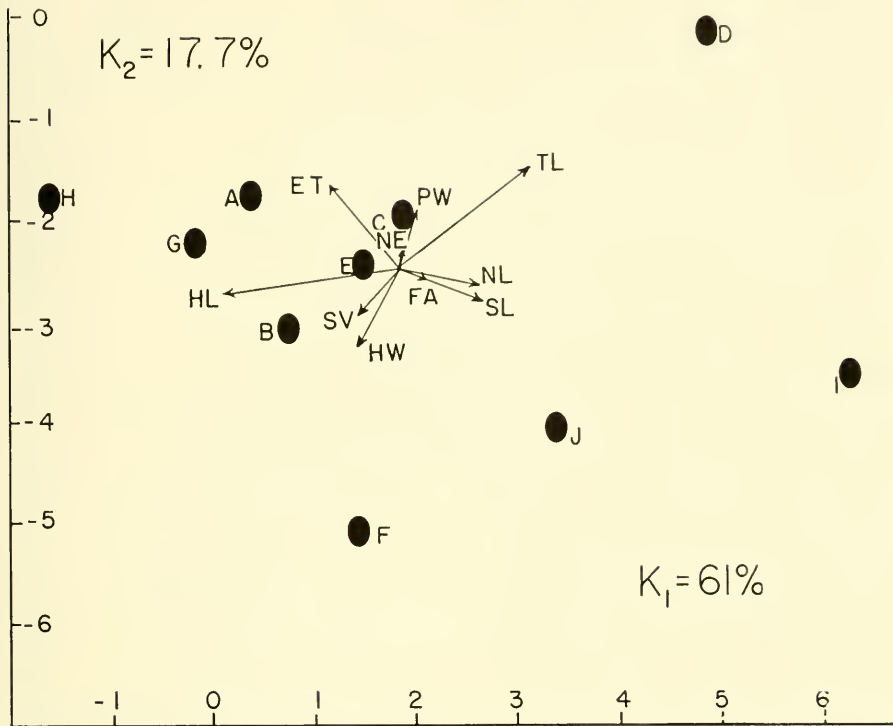
FIGURE 7. The mean of the female samples of each subspecies is shown on the first (K_1 = 61.0%) and second (K_2 = 17.7%) discriminant axes (table 4). Symbol and vector labels are as in figure 4.

successive root is significantly smaller than the next larger. We offer here a detailed summary of the variation in males and females of the total sample with respect to all roots (tables 5–7), and we have used Kaiser's rule of thumb for the comparisons of the subspecies. More complete analyses will be presented elsewhere.

SEXUAL DIMORPHISM.

The roots of the variance–covariance matrix may be compared to provide an estimate of the amount of variation in each group. The females (table 6) are more variable than the males:

$$\Sigma\lambda = 35.62 \text{ in } \female ; \ \Sigma\lambda = 24.80 \text{ in } \male \text{ where } i = 1. \ 10.$$

The per cent variability in each root indicates that the principal factors underlying variation in males and females are similar.

The correlation matrix of males and females is shown in table 5. All the coefficients (r) for the male measurements show a high positive correlation

$K_4 = 6.6\%$

J

NL

I

H

TL

HL

ET G

5

HW

B E

SV

NE SL

FA C

4

D A

PW

$K_3 = 10.4\%$

F   -15   -14   -13
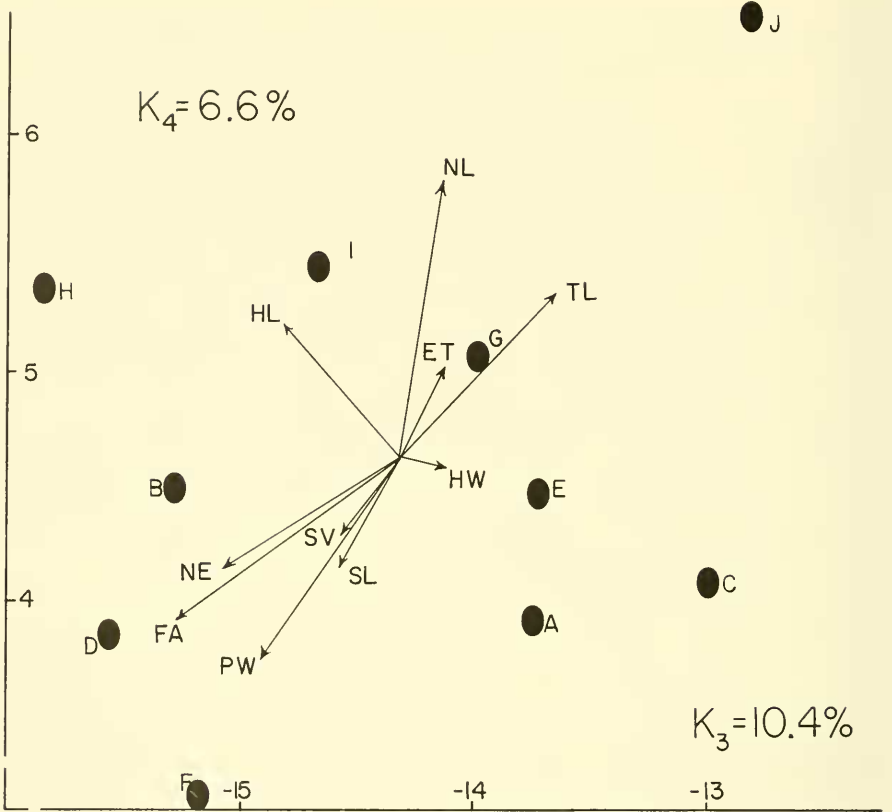
FIGURE 8. The mean of the female samples of each subspecies is shown on the third (K_3 = 10.4%) and fourth (K_4 = 6.6%) discriminant axes (table 4). The symbol and vector labels are as in figure 4.

with each other at $P \leqslant 0.01$. The measurements of females exhibit high values of r except for: shank length—eye–tympanum and toe length—eye–tympanum; these values are not significant at $P = 0.05$. The number of significant r's for both sexes indicates that all parts of an animal tend to increase in size simultaneously. The exceptions involve eye–tympanum and represent the distance between two organs, both of which are increasing in size; one might expect that the distance between the two would decrease, remain constant, or slowly increase. The latter is most probably the case in this instance, resulting in the low values for r.

Males. The head measurements are more highly correlated than expected with each other than with other measurements except that pad width is more correlated with nostril–lip and head length with snout–vent. The former exception is present in both sexes; the latter can be explained by the fact that
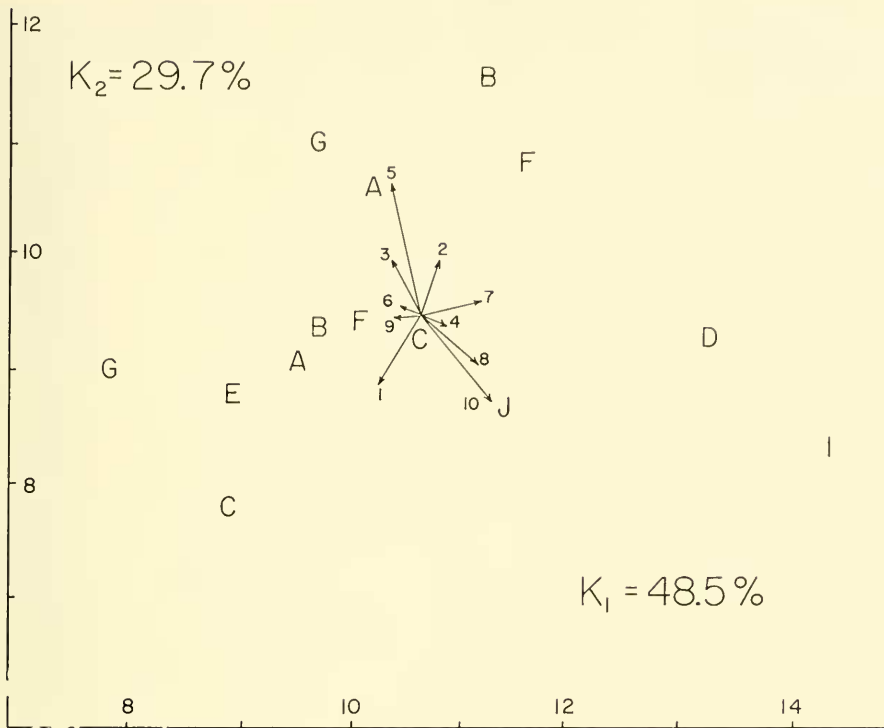
FIGURE 9. The mean of the male and female samples of each subspecies is shown on the first ($K_1 = 48.5\%$) and second ($K_2 = 29.7\%$) discriminant axes to indicate the simultaneous variation. The vector labels are as in figure 4. The symbols are as in figure 11.

head length is a component of snout–vent and the two vary in proportion to each other.

The appendages and general size (snout–vent) measurements are most highly correlated with each other as expected. The highest correlation coefficient for the male measurements is that of shank length with forearm length indicating that both anterior and posterior appendages are closely related in their relative sizes.

Females. The head measurements are generally highly correlated with other head measurements with two exceptions: nostril–lip with snout–vent and pad width with nostril–lip. The former exception indicates that females tend to have a taller face in relation to their overall length. The latter exception was also present in males.

The appendage measurements are highly correlated with each other and with those measurements which give an indication of general size. The highest correlation coefficients for the female measurements are: head width with head

TABLE 5. *The correlation coefficients of 10 measurements of 90 females of* Hyla regilla *(roman face type) and 454 of* Hyla regilla *(italics). For 88 df,* $P_{0.05} \geqslant 0.205$; $P_{0.01} \geqslant 0.269$. *For 452 df,* $P_{0.05} \geqslant 0.093$; $P_{0.01} \geqslant 0.120$.

	Measurement number and letter code / Measurement	1–NL Nos-tril–lip	2–NE Nos-tril–eye	3–ET Eye–tym-panum	4–PW Pad width	5–HL Head length	6–HW Head width	7–SV Snout–vent	8–SL Shank length	9–FA Fore-arm length	10–TL Toe length
Females	1–NL		0.73	0.48	0.67	0.83	0.72	0.78	0.71	0.71	0.66
	2–NE	0.66		0.48	0.49	0.80	0.74	0.74	0.69	0.69	0.59
	3–ET	0.50	0.51		0.38	0.50	0.37	0.35	0.30	0.32	0.22
	4–PW	0.62	0.31	0.42		0.59	0.55	0.63	0.62	0.62	0.62
	5–HL	0.82	0.82	0.45	0.47		0.83	0.85	0.80	0.81	0.70
	6–HW	0.74	0.71	0.33	0.51	0.89		0.81	0.80	0.80	0.70
	7–SV	0.85	0.69	0.35	0.56	0.89	0.86		0.87	0.87	0.85
	8–SL	0.72	0.60	0.19	0.47	0.82	0.82	0.85		0.87	0.87
	9–FA	0.69	0.63	0.28	0.44	0.76	0.70	0.80	0.54		0.85
	10–TL	0.77	0.56	0.18	0.61	0.77	0.78	0.89	0.86	0.74	
Sum r →	Males	7.29	6.95	4.40	6.17	7.71	7.32	7.75	7.53	7.54	7.06
	Females	7.37	6.49	4.21	5.41	7.69	6.34	6.74	6.87	6.58	6.16

Males (spanning column header across measurement columns)

length, head length with snout–vent, and snout–vent with toe length. The value for each of these is 0.89 which is equal to the high value for the males.

Comparison of males and females. If each measurement was exactly correlated with all the other measurements, the sum of the correlation coefficients for a measurement with respect to x measurements should be equal to $(x) \times (1.00)$. With 10 measurements the sum of r for a perfect correlation is 10. Such a sum was calculated for males and females and shown in table 5. As the above analysis of single values for r indicated, males and females differ substantially with respect to the correlation coefficients.

If the values for Σr are arranged in order of magnitude, the largest Σr for both males and females is snout–vent (7.75 males; 7.74 females). This value indicates that the snout–vent measurement is most closely correlated with all the other measurements taken. Head length is second in both males and females (7.71 males; 7.69 females). At this point the numerical order for the sum of r differs between males and females. Those values which fall in the same numerical position for both males and females are: snout–vent [1st], head length [2nd], nostril–eye [8th] (6.95 males; 6.49 females); pad width [9th] (6.15 males; 5.41 females); and eye–tympanum [10th] (4.39 males; 4.21 females). In each of the above cases and, in fact, in seven of the ten measurements the

TABLE 6. *Factor analysis of 454 males of Hyla regilla. For each principal component axis the roots of the variance–covariance (W) and the correlation (R) matrix and the direction cosines of the 10 measurements are given. The angle of deviation from 0° (isometry) of the first axis is 8°49'. The angle of separation from the female vector in the first axis is 3°26'. The second is 14°10', and the third and fourth are greater than 40°0'.*

	Principal Component Axis									
	1	2	3	4	5	6	7	8	9	10
Roots of										
W (λ)	22.07	1.11	0.74	0.41	0.20	0.13	0.06	0.03	0.03	0.02
Per cent										
of total	89.0	4.5	3.0	1.7	0.8	0.5	0.2	0.1	0.1	0.1
Roots of R	7.12	0.98	0.59	0.37	0.24	0.23	0.14	0.13	0.11	0.09
Direction cosines										
Nostril–lip	0.326	−0.166	0.092	−0.446	0.648	−0.234	0.223	0.264	−0.178	−0.173
Nostril–eye	0.311	−0.218	−0.382	−0.351	−0.206	0.727	0.087	0.078	−0.028	−0.006
Eye–tympanum	0.182	−0.817	0.095	0.530	−0.006	−0.030	0.074	0.039	0.025	−0.040
Pad width	0.272	−0.044	0.831	−0.290	−0.354	0.087	−0.083	−0.085	0.023	0.036
Head length	0.346	−0.125	−0.209	−0.144	0.124	−0.222	−0.434	−0.474	−0.072	0.559
Head width	0.331	0.037	−0.275	−0.108	−0.570	−0.553	0.322	0.243	0.078	0.051
Snout–vent	0.352	0.142	−0.051	0.076	0.158	0.008	−0.141	−0.129	0.817	−0.350
Shank length	0.342	0.237	−0.025	0.245	−0.018	0.032	0.310	−0.587	−0.417	−0.397
Forearm	0.342	0.205	−0.035	0.256	−0.060	0.014	−0.631	0.462	−0.331	−0.227
Toe length	0.321	0.348	0.146	0.387	0.209	0.229	0.352	0.240	0.072	0.567

males have larger correlation coefficients than the females. The value of the summed r's for the eye–tympanum measurement is the smallest value for both males and females, again indicating a low degree of correlation between this measurement and the others.

The first principal axis of the correlation matrix includes 68.7 per cent of the variability for females, 71.2 per cent for males. The magnitude of the deviation of the angle of the sample vector from the isometric or expected vector is 10°14' in females and 8°49' in males; the difference is 1°25'. The magnitude of the deviation of the angle between the male sample vector and the female sample vector can be calculated by: $\cos \phi = U_{1,1} U_{2,1} + U_{1,2} + U_{2,2} + \ldots U_{1,10}, U_{2,10}$, where $U_{1,i}$ = male direction cosines ($i = 1, 10$), $U_{2,i}$ = female direction cosines ($i = 1, 10$). This deviation is calculated at 3°26' in the first axis. The difference between 1°25' and 3°26' is surely attributable to further shape differences between males and females. Since all measurements do not increase equally it is apparent that all of the first principal axis is not a size component. The coefficients of the eye-to-tympanum length (0.178 in females, 0.182 in males) and the toe pad width (0.243 in females and 0.272 in males) are certainly less than expected. Both males and females seem to grow longer faster (coefficients of snout–vent (0.366 in males and 0.352 in females) than the other parts. Apparently the head length grows faster in females (0.361)

TABLE 7. *Factor analysis of 90 females of* Hyla regilla. *For each principal component axis the roots of the variance–covariance* (W) *and correlation* (R) *matrix and the direction cosines of the 10 measurements are given. The angle of deviation from 0° (isometry) of the first axis is 10°14'. The angle of separation from the male vector in the first axis is 3°26'; the second, 14°10'; the third and fourth are greater than 40°0'.*

	Principal Component Axis									
	1	2	3	4	5	6	7	8	9	10
Roots of										
W (λ)	31.69	1.76	0.97	0.61	0.26	0.16	0.08	0.04	0.03	0.02
Per cent										
of total	89.0	4.9	2.7	1.7	0.5	0.5	0.2	0.1	0.1	0.1
Roots of R	6.87	1.05	0.79	0.47	0.26	0.20	0.17	0.08	0.06	0.04
Direction cosines										
Nostril–lip	0.342	−0.117	0.130	0.019	0.502	0.418	−0.605	0.196	0.100	−0.103
Nostril–eye	0.301	−0.222	−0.494	−0.039	−0.451	0.586	0.162	0.139	−0.144	−0.029
Eye–tympanum	0.178	−0.829	−0.013	−0.106	0.261	−0.322	0.293	0.096	0.029	−0.046
Pad width	0.243	−0.197	0.781	0.028	−0.490	0.128	−0.028	−0.180	−0.020	−0.042
Head length	0.361	−0.020	−0.238	−0.076	−0.061	−0.124	−0.174	−0.585	0.452	0.459
Head width	0.345	0.112	−0.122	−0.171	−0.367	−0.552	−0.394	0.473	−0.063	−0.042
Snout–vent	0.366	0.129	0.011	0.050	0.229	−0.094	0.053	−0.252	−0.814	0.239
Shank length	0.328	0.292	0.006	−0.540	0.136	−0.009	0.269	−0.222	0.109	−0.603
Forearm	0.310	0.086	−0.109	0.810	0.004	−0.160	0.116	−0.087	0.135	−0.405
Toe length	0.339	0.299	0.213	0.035	0.166	0.088	0.496	0.464	0.257	0.432

than in males (0.346), while the limbs certainly grow faster in males (shank, 0.342; forearm, 0.342) than in females (shank, 0.327; forearm, 0.310). These deviations from isometry and the amount of variation in axes other than the first suggest that approximately one-third of the variation in *Hyla regilla* is variation in shape.

The second principal axis characteristically represents the differences in shape of males and females, and 10.5 and 9.8 per cent of the variation are present here. Appendage lengths, total lengths, and head width have positive coefficients, while head lengths, face shapes, and toe pad width have negative coefficients. This axis is responsible for 10.5 and 9.8 per cent of the variation in females and males, respectively; a major portion $|(-0.829)^2 = 68.7$ per cent in females; $(-0.817)^2 = 66.7$ per cent in males] of the variability in this axis is the result of the large decrease in growth rate of the eye-to-tympanum measurement. The deviation between the angles of the second principal axes in males and females is 14°10'.

The third principal component represents 7.9 per cent of the variation in females and 5.9 per cent in males; pad width and nostril-to-eye distance are largely responsible for the shape variation in the third axis. The magnitude of the deviation between the male and female third principal axis is 14°7'. The first three axes account for 87.1 per cent of the variation in females and 86.9

per cent of the variation in males, and the differences between males and females are very little.

Considerable differences between the shape of males and females become apparent in the fourth axis where 2.6 per cent of the variability is found in females and 2.4 per cent in males. In males a decrease in the rate of growth of the nostril–lip and the nostril–eye measurements, and an increase in the rate of growth of the eye–tympanum distance and toe length account for 75.3 per cent of the variation in this axis. Decrease in the growth rate of shank length and increase in forearm length account for 91.8 per cent of the variation in the fourth axis in females. The angle of deviation between male and female axes is more than 40° which, to say the least, is enormous.

Less than 10 per cent of the total variation in 10 measurements is found in the last six axes. While these represent little of the total variation, they are of interest in distinguishing components of the total variation between males and females. The differences between the coefficients of growth of the forearm length in males when compared with females in the sixth and seventh principal axes and in shank length in the eighth and ninth axes suggest that additional rotation of both the Quartimax and Varimax type will be of use. Since we are concerned here with differences between subspecific groups rather than a detailed analysis of males and females, we reserve the rotated matrices analysis for future presentation.

Factor Analysis of Subspecies:

Some of the details of these factor analyses are summarized in tables 8–17 and in the discussion of each subspecies. The roots of the covariance matrix (W) may be compared to provide an estimate of the amount of variation in each group and to some extent the nature of that variation. Two sets of latent roots may be compared by Hotelling's T^2 test (1931) or several other tests. When many groups are involved the problem of large beta error arises, and the logical solution is the multivariate discriminate analysis used in figures 3–9 and tables 3 and 4. The obvious similarity between the latent roots of the total males and the total females and the differences between the latent roots of the several subspecies may indicate the usefulness of the latent roots in determining size and shape differences between two adjoining subspecies and in testing the membership of a geographically intermediate population (Rao, p. 308) or of a single individual (Cooley and Lohnes, p. 137).

We have provided the direction cosines for each subspecies for the first two axes following the general rule of Kaiser, who recommends use of those roots greater than 1.0 (the third axis never reaches a value greater than 1.00). From 59.0 per cent of the variance in *H. r. lafrentzi* to 74.6 per cent in *H. r. palouse* can be explained in the first principal component axis and from 6.7 per cent in *H. r. deserticola* to 15.4 per cent in *H. r. lafrentzi* can be explained in the second
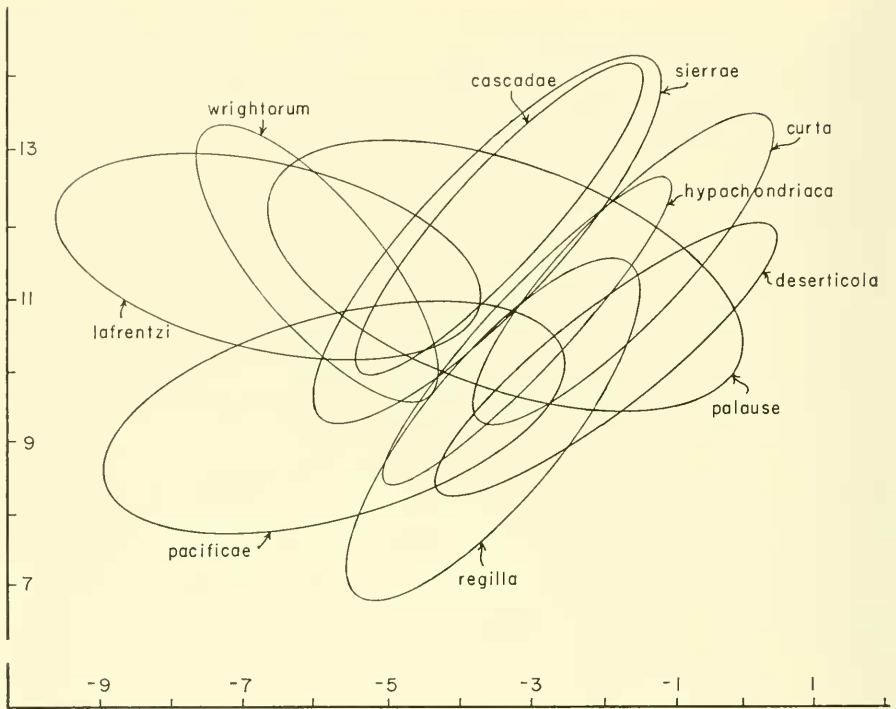
Figure 10. Equal frequency ellipses of 95 per cent of the variation of the male samples of each of the subspecies is shown on the first and second discriminant axes. The axes are the same as those shown in figure 4. The ellipses are not those of the principal axes of the factor analysis.

principal component axis. Combined, the first two principal components contain from 88.5 per cent in *H. r. wrightorum* to 71.0 per cent in *H. r. curta*.

First principal axis:

If all parts of the animal grow at equal rates (isometry), we would expect the value of the direction cosines of the first principal axis would be equal and would be $\sqrt{1/10} = 0.316$. The deviation of each of the direction cosines from 0.316 indicates the direction and amount of allometry in each measurement in each of the subspecies. The total allometry can be estimated by calculating the magnitude of the deviation of the sample from the expected value. The greatest deviation is that of *H. r. lafrentzi* ($17°55'$), the least is found in *H. r. deserticola* ($6°10'$). All of these deviations are large enough to suggest that they differ significantly from isometry; the appropriate statistical tools are available and will be used as soon as the computer program can be developed. The coefficient of growth of the eye–tympanum distance is smallest in *H.*

r. lafrentzi (−0.039) and largest in *H. r. wrightorum* (0.288). The pad width growth rate is less than expected (on the basis of isometry) in all forms except *H. r. palouse*. Snout-vent and limb length growth ranges appear to be about equal to each other in *H. r. palouse, H. r. regilla, H. r. pacifica, H. r. wrightorum,* and *H. r. deserticola*. Snout-vent grows faster in *H. r. hypochondriaca* and *H. r. lafrentzi* and slower in *H. r. curta*. Forearm growth is faster in *H. r. lafrentzi* and slower in *H. r. cascadae*. Shank length increases faster in *H. r. sierra, H. r. pacifica*, and *H. r. curta* and slower in *H. r. hypochondriaca*. Toe length increases fastest in *H. r. regilla* and slowest in *H. r. cascadae*. The growth rate of the nostril–lip distance is about equal to that of the nostril–eye distance in *H. r. cascadae, H. r. hypochondriaca,* and *H. r. deserticola* while they are greatly different in *H. r. wrightorum* and *H. r. lafrentzi*.

Second principal axis:

This axis characteristically represents the differences in shape of the different groups. Total males are characterized by positive coefficients with respect to appendage and total lengths, while head lengths and thus face shapes and toe pad width have negative coefficients. Obvious changes in the direction (as shown by change of sign from total males) of growth include: nostril–lip in *H. r. regilla*, nostril–eye in *H. r. cascadae* and *H. r. regilla*, pad width in *H. r. regilla*, head–width in *H. r. regilla* and *H. r. lafrentzi*, snout–vent in *H. r. wrightorum*, shank length in *H. r. regilla* and *H. r. hypochondriaca*, and forearm length in *H. r. palouse* and *H. r. cascadae*. Obvious changes in rate of growth include: nostril–lip in *H. r. pacifica*, nostril–eye in *H. r. regilla, H. r. pacifica, H. r. wrightorum,* and *H. r. lafrentzi*, pad width in *H. r. sierra, H. r. wrightorum,* and *H. r. curta*, head width in *H. r. deserticola* and forearm length in *H. r. pacifica* and *H. r. hypochondriaca*.

COMMENT. The differences in shape and form of the several subspecies herein described are considerable. Factor analysis provides a method of describing some of these differences as well as describing the differences between males and females. The most stable measurement appears to be the toe length measurement. The most stable factor is, of course, that represented by the first principal component axis (size). The subspecies most similar to the total male population of *Hyla regilla* are *Hyla regilla palouse, H. r. cascadae, H. r. sierrae,* and *H. r. hypochondriaca*, as is illustrated by comparing the tables and by comparing these subspecies to the grand mean in figure 4.

Hyla regilla regilla Baird and Girard.

Hyla regilla (Baird and Girard), 1852. Cotypes (2): 9182, United States National Museum (USNM), Puget Sound, Washington, C. J. Pickering. 15409 (USNHM), Sacramento River (restricted to Sacramento County, California). U. S. Exploring Expedition, 1841.

Hyla scapularis (Hallowell), 1852. Number 1978, Academy of Natural Sciences of Philadelphia, collected in the Oregon Territory, 1852, by Shumard. Restricted to Vancouver, Washington.

HOLOTYPE. 9182, U. S. National Museum (USNM), Puget Sound, Washington, C. J. Pickering.

PARATYPES. None in existence.

DIAGNOSIS. One of the smallest subspecies of the *Hyla regilla* complex attaining a mean size of 32 mm. head–body length; dorsal skin pustulate; ventral granulation coarse; head narrow; tympanum small, less than one-half the diameter of the eye; minute vestige of web between fingers, toes three-quarters webbed; tibiotarsal articulation to posterior edge of eye or slightly beyond.

DESCRIPTION OF THE HOLOTYPE. Adult male. Nostril to edge of lip, 2.3 mm.; nostril to anterior edge of eye, 2.5 mm.; posterior edge of eye to anterior edge of tympanum, 1.0 mm.; width of pad on third digit, 1.1 mm.; length of head, 10.0 mm.; width of head, 10.4 mm.; snout–vent length, 29.5 mm.; tibia, 14.0 mm.; length of forearm, 7.1 mm.; length of fourth toe, 12.2 mm.

Head narrow at angle of jaw, sloping slowly forward to form a rounded snout; in lateral profile snout rounded, extending beyond the mouth; eyes are fairly prominent, protruding beyond outline of jaw; nostrils prominent, surrounded by raised portions of tissue; line between the eye and nostril slightly concave; nostril approximately the same distance from the eye as from the median anterior of lip; tympanum small, approximately equal to one-half the diameter of the eye.

Vomerine teeth small but visible lying between the choanae; tooth groups closer to the choanae than to each other; choanae slightly larger than the size of each tooth group; tongue is generally circular in shape, free posteriorly for about one-third of its length; vocal sac small, folds of skin almost absent because of extreme age of specimen. A moderate to light supratympanic fold extends to the insertion of the forearm; the skin above appears pustulate, becoming granular at the sides; entire abdomen and underside of thigh and arm with granulation; skin granular in anal region; granulation continues into the vocal sac.

Fingers slender with a vestige of web; thickened dermal ridges remain, extending to the termination disks; disks moderately large, the largest being easily greater than one-half the diameter of the tympanum; moderate nuptial callosity exists at the base of the first finger, and each finger has at least one or more tubercles, the total number not being great; a few small palmar tubercles present.

Foot moderately elongate, the part from the tarsometatarsal articulation to the tip of the longest toe extending about three-quarters of the way up the femur; inner metatarsal tubercle small, but easily recognized; the outer tubercle about one-third the size of the inner and may be confused with other foot tubercles; small tubercles distributed on each toe and on the foot; toe webbing extends for about three-quarters of the length of the toes, extended by thickened dermal ridges; toe disk distinctly smaller than finger disks. Legs short, tibio-

tarsal articulation extending to the posterior edge of the eye; tarsal fold well defined.

COLOR IN ALCOHOL. Above, on limbs and body, a dark brown color (probably green in life). Age has obscured any dorsal markings which might have been present. It appears that an eye stripe may possibly have been present since coloration in this area is lighter, but the preservation medium has successfully removed any other traces of body coloration and pattern.

The original type of *Hyla scapularis* Hallowell is an adult male, 1978, Academy of Natural Sciences of Philadelphia. The following differences are noted between it and the holotype (9182 USNM) of *Hyla regilla regilla* described above: Nostril to edge of lip, 2.8 mm.; nostril to anterior edge of eye, 3.0 mm.; posterior edge of eye to anterior edge of tympanum, 1.6 mm.; width of pad on third digit, 2.0 mm.; length of head, 12.1 mm.; width of head, 13.9 mm.; snout–vent length, 38.0 mm.; tibia, 20.2 mm.; length of forearm, 9.1 mm.; length of fourth toe, 16.4 mm. The vocal sac is slightly more evident in 1978 and only a minute vestige of web is present between the digits; toe webbing is slightly reduced, the toes about one-half webbed.

VARIATION. The range of variation present in the males comprising the data for the biometrical analysis of this subspecies is shown in table 8. The SDNHM series used for the biometrical analysis of this subspecies follows very closely the description of the holotype. Some variation in the amount of toe webbing present was observed. The SDNHM series showed greater amounts of such webbing. The females of this series show the same characters as the male with the exception of size; the females were generally larger.

FACTOR ANALYSIS OF *Hyla regilla regilla*. The primary variation in the first axis accounts for 70.5 per cent of the total and is largely attributable to those measurements which show increases in the size of the animal (table 8). Factors two through five have direction cosines which differ in sign indicating a shape variation. In axes three through five those measurements which show an increase in the size of the head and cranial cavity are responsible for most variation. Factors six through ten show secondary variation in limb and body size. The correlation matrix for this subspecies shows most measurements to be highly correlated, $P < 0.01$. The only nonsignificant correlation is between nostril–eye distance and eye–tympanum distance.

RANGE. *Hyla regilla regilla* exists in the Rogue, Umpqua, and Willamette valleys and the Puget Trough of Oregon, Washington, and southern British Columbia. The subspecies has its southern limit at Evans Creek, Oregon (just north of Medford); the northern limit appears to be Vernon, British Columbia. The subspecies exists in an easterly direction up into the foothills of the Cascade Mountains; the western limit is the range of mountains along the Pacific Coast.

MATERIAL EXAMINED. (210): Fort Lawton, Washington: AMNH 299-302,

TABLE 8. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 30 adult males of* Hyla regilla regilla *are listed with the roots* (λ) *of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code Measurement	1–NL Nos- tril– lip	2–NE Nos- tril– eye	3–ET Eye– tym- panum	4–PW Pad width	5–HL Head length	6–HW Head width	7–SV Snout– vent	8–SL Shank length	9–FA Fore- arm	10–TL Toe length
Female mean	2.71	2.98	1.54	1.53	11.44	12.12	36.49	17.80	8.67	15.34
Male mean	2.54	2.54	1.28	1.40	10.11	10.90	32.13	15.38	7.76	13.23
Standard deviation	0.25	0.24	0.16	0.23	0.82	0.95	2.58	1.49	0.80	1.37
Direction cosines										
First axis	0.288	0.266	0.239	0.262	0.342	0.338	0.347	0.348	0.354	0.350
Second axis	0.169	−0.434	0.622	0.468	−0.128	−0.264	0.113	−0.246	−0.123	0.053
Roots λ	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.05	1.07	0.56	0.50	0.34	0.18	0.15	0.08	0.05	0.03
Variance component	11.50	1.01	0.30	0.13	0.09	0.05	0.03	0.02	0.01	0.01
Per cent of total	87.5	7.7	2.3	1.0	0.7	0.4	0.2	0.2	0.1	0.1

53320. Evans Creek, Oregon: USMVZ 17163, 64, 66-17170. Eugene, Oregon: SDNHM 53171-53264. Corvallis, Oregon: SDNHM 53265-53296. Chilliwack, British Columbia: SDNHM 53297-53326. Portland, Oregon: SDNHM 53327-53344. Abbotsford, British Columbia: SDNHM 53431-53453.

Hyla regilla deserticola Jameson, Mackey, and Richmond, new subspecies.

Hyla regilla (Baird and Girard), 1852. Cotypes (2): 9182 United States National Museum (USNM), Puget Sound (restricted to Fort Vancouver), Washington, C. J. Pickering. 15409 (USNM) Sacramento River (restricted to Sacramento County, California), U. S. Exploring Expedition, 1841.

HOLOTYPE. Adult male, SDNHM 54176, collected San Borjas, Baja California, by D. L. Jameson on November 25, 1961.

PARATYPES. SDNHM series 54166-54175.

DIAGNOSIS. The smallest subspecies of the *Hyla regilla* complex, attaining a mean size of 32 mm. head–body length; dorsal skin pustulate; ventral granulation fine; head narrow; tympanum diameter less than one-half the diameter of eye; minute vestige of web present between fingers; toes three-quarters webbed; tibiotarsal articulation to posterior edge of eye.

DESCRIPTION OF THE HOLOTYPE. Adult male. Nostril to lip, 2.7 mm.; nostril to edge of eye, 2.9 mm.; posterior edge of eye to anterior edge of tympanum,

1.5 mm.; width of pad on second digit, 1.4 mm.; length of head, 11.4 mm.; width of head, 10.9 mm.; snout-vent length, 34.9 mm.; tibia, 15.8 mm.; length of forearm, 8.1 mm.; length of fourth toe, 13.8 mm.

Head moderately narrow at the angle of jaw sloping forward to form a rounded snout; tip of snout rounded in the lateral profile and extending slightly beyond the mouth; eyes moderately prominent but protruding beyond outline of the jaw; nostrils about equally distant from the edge of the upper lip and eye; line between the eye and nostril straight; tympanum small, approximately less than one-half of the diameter of the eye.

Vomerine teeth present, situated wholly between the choanae and lying closer to the choanae than to each other; choanae moderately large and will easily include a tooth group; tongue elliptical in shape, free posteriorly for one-fifth of its length; vocal sac medial, single, evident on the chin by ample folding of skin.

A light supratympanic fold present extending from the posterior edge of the eye to the insertion of the forearm. The skin above pustulate becoming granular at the sides; entire abdomen and underside of thigh and arms finely granular; granulation continues well beyond the breast fold up into the vocal sac; skin granular in anal region.

The fingers moderately elongate with no vestige of web remaining between them; dermal thickening of the edges of the digits extending to the disks is present; disks distinct, small, elliptical in shape but larger than toe disks; width of the largest finger disk approximately equal to the diameter of the tympanum; moderately large nuptial callosity exists on the inside base of the first finger; both the finger and the palm with many tubercles of varying size; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe extends slightly more than halfway up the tibia; both the inner and outer metatarsal tubercles are small. Toes one-half webbed, webbing continued to the disks in the form of thickened dermal ridges; toe disks small, just slightly wider than the width of the toes; the fourth toe of the left foot has been cut, pad is no longer present; tarsal fold is slight but evident. Legs short, tibiotarsal articulation extending to the posterior edge of the eye.

COLOR IN ALCOHOL. Above, on limbs and body, dark gray (probably a shade of gray or brown in life). A dark line beginning below the nostril and widening rapidly runs through the eye, widens involving the tympanum, becomes discontinuous at the insertion of the forearm, and is continued down the sides as a series of dark spots. A discontinuous line runs around the upper lip bordered above by a thin cream color.

VARIATION. The ranges of variation present in the males of this subspecies are seen in table 9. The five males and one female of the paratype series show marked similarity to the holotype. Some variation in tibiotarsal articulation is present; it tends to be slightly greater in several paratypes. Dorsal skin also somewhat smoother in the paratype series. The female is similar to the males

Table 9. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 133 adult males of* Hyla regilla deserticola *are listed with the roots (λ) of the correlation matrix and the roots and per cent of the total of variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nos-tril–lip	Nos-tril–eye	Eye–tym-panum	Pad width	Head length	Head width	Snout–vent	Shank length	Fore-arm	Toe length
Female mean	2.96	3.17	1.79	1.57	12.09	12.62	37.35	17.59	8.87	14.63
Male mean	2.61	2.66	1.39	1.28	10.44	11.12	32.00	15.21	7.64	12.57
Standard deviation	0.27	0.25	0.20	0.24	0.87	1.42	3.18	1.57	0.84	1.42
Direction cosines										
First axis	0.313	0.308	0.229	0.297	0.341	0.287	0.347	0.335	0.343	0.344
Second axis	−0.122	−0.033	−0.915	0.059	0.040	0.310	0.043	0.117	0.116	0.128
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.44	0.67	0.44	0.43	0.37	0.25	0.15	0.11	0.08	0.06
Variance component	16.27	0.95	0.54	0.19	0.14	0.08	0.03	0.02	0.02	0.01
Per cent of total	89.2	5.2	3.0	1.0	0.8	0.4	0.2	0.1	0.1	0.1

in the characters noted with the exception of snout–vent length, the female being larger.

Factor analysis. The first axis shows primary variation in snout–vent, toe length, forearm length, head length, and shank length. The direction cosines for this axis are all positive, indicating size variation or a growth trend responsible for 74.4 per cent of the variation. The second and third factors show primary variation in head size, eye to tympanum, and length of limbs. Factors four and five exhibit variation in body and limb size. The sixth and seventh axes show variation in head height and limb size. Factors eight through ten present variation in limb and body size. The direction cosines of the last nine axes differ in sign and represent a shape variation.

Range. *Hyla regilla deserticola* is found in isolated localities in Nevada, Arizona, Baja California Norte, and California. The subspecies is present in the low, somewhat arid regions of Nevada but absent on the high northern plateau of this state. The northern limit of the range in Nevada is Jarbidge, Elko County. The range in Arizona seems to be limited to the border areas near the Lake Mead National Recreation area. The distribution in California includes the great inland valley; the northern limit exists near Corning, California. The subspecies is found south of the Tehachapi Mountains near Willow Springs Road

in the Mojave Desert and sporadically along the east face of the coast range in southern California and in the north central region of Baja California and on the Pacific coastal islands. On the western coast of Baja California some intergradation of *Hyla regilla deserticola* and *Hyla regilla hypochondriaca* has occurred, specifically at San Quintín and Rosario.

MATERIAL EXAMINED. (589): Tehachapi Mountains, California: CAS 39003-39078. Las Vegas, Nevada: CAS 33434, 33440, 36856-36958. Santa Cruz Island, California: CAS 36137-36148, 45233-45302. Santa Catalina Island, California: CAS 3550-35566, 39125-39166, 39855. Santa Rosa Island, California: CAS 36103-36119. Panamint Mountains, California: CAS 65342-65377. Coalinga, California: SU 7521-7526. Wheeler Ridge, California: SU 20309-20322. Cottonwood Creek, California: SU 6452-6457. Fort Mojave, California: SU 14081-14122. Willow Springs, California: SU 18375-18387. San Quintín, Baja California: SU 9693-9703. Saratoga Hot Springs, California: SU 13074-13081 (intergrade between *Hyla regilla deserticola* and *Hyla regilla sierrae*). Pahrump Slough, Nevada: SU 7527-7536. Afton Station, California: SU 9413-9416 (intergrade between *Hyla regilla deserticola* and *Hyla regilla sierrae*). Corning, California: SDNHM 53770-53781. Calamajue, Baja California: SDNHM 54087-54165. San Borjas, Baja California: SDNHM 54166-54176. Carrizo, California: SDNHM 54948-54960. Scissors Crossing, California: SDNHM 54961-54982 (intergrade between *Hyla r. deserticola* and *Hyla r. hypochondriaca*). Las Vegas, Nevada: UCMVZ 8924, 8927, 19509-19512, 19515, 19518, 19538, 19541, 19543. Beatty, Nevada: UCMVZ 12975, 12984, 12988-12989, 12998. Jarbridge, Nevada: UCMVZ 65565, 11956.

Hyla regilla curta Cope, new combination.

Hyla curta (Cope), 1867. Cotypes (19) 5293(19), United States National Museum (USNM). In a spring at Soria, 15 miles north of Cape San Lucas, Baja California, Mexico, J. Xantus, August 10, 1859.

Hyla regilla laticeps (Cope), 1889. Cotypes (7) 5308(7), United States National Museum (USNM). Cape San Lucas, Baja California, Mexico. J. Xantus.

COTYPES. (19) Subadults, number 5293 USNM, collected in a spring at Soria, 15 miles north of Cape San Lucas, Baja California, Mexico, by J. Xantus, August 10, 1859.

PARATYPES. None designated.

DIAGNOSIS. A moderate to small-sized subspecies of the *Hyla regilla* complex, attaining an average size of 34 mm. head-body length; dorsal skin smooth, head narrow, tympanum diameter less than one-half the diameter of the eye; no vestige of web present between fingers; large, flattened nuptial callosity on base of first finger; foot three-quarters to fully webbed; tibiotarsal articulation to within or beyond eye.

DESCRIPTION OF THE COTYPES. All cotype specimens subadult, the largest having a snout-vent length of 24.0 mm. Head fairly narrow at the angle of

the jaw sloping abruptly to give a rounded snout, in lateral profile snout appears very rounded and extends well beyond the mouth; eyes fairly prominent protruding beyond the outline of the jaw, nostril nearer to median anterior edge of mouth than to the eye; tympanum small, its diameter being less than one-half the diameter of the eye; the line between the eye and nostril slightly concave.

Vomerine teeth groups moderately large lying wholly between the choanae, being slightly closer to each other than to the choanae; choanae are fairly large and easily capable of including two tooth groups; tongue broadly elliptical, free posteriorly for about one-third of its length; vocal sac not present due to subadult status of specimen.

A light to moderate supratympanic fold extends from the posterior edge of the eye to the insertion of the forearm. The skin above is practically smooth (minutely corrugate), becoming finely granular well down on the sides; entire abdomen and underside of thigh with small but distinct granules; granulation generally lacking on skin of breast fold and underarm; skin granular in anal region.

No vestige of web present between the fingers; very slight evidence of dermal thickening on the edges of digits extending to the disks. Disks distinct, elliptical, that on the third finger largest, its length being one-half the diameter of the tympanum; a large but flattened nuptial callosity on the base of the first finger; remainder of finger and palm contain moderate-sized tubercles; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe reaching one-half of the way up the tibia; inner metatarsal tubercle small, the outer one not present. Toes one-half webbed, clearly defined tarsal fold; foot generally smooth; a tibiotarsal articulation to the posterior edge of the eye or beyond.

COLOR IN ALCOHOL. Above and on limbs gray to light brown, dorsal markings present but fading. A dark stripe beginning slightly beyond the nostril runs through the eye, widens involving the tympanum, and ends at the insertion of the forearm. A thin dark line bordered above in cream runs around the upper lip.

VARIATION. For the range of variation present in the males comprising the data for the biometric analysis of this subspecies see table 10. The animals used for biometrical analysis of this subspecies follow closely the description of the cotypes with the following exceptions. The vocal sac is present, these animals being adult males. The toes may be webbed to three-quarters of their length. The females of the subspecies show the same characters as the male counterparts and generally vary only in size; females are larger.

FACTOR ANALYSIS. This subspecies exhibits similar trends of growth and shape variation to the desert subspecies. Primary variation (60.0 per cent) in the first axis is based on a general increase of all characters with the limbs and head having the greatest rate of increase. Elongation of the limbs and in-

TABLE 10. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 38 adult males of* Hyla regilla curta *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nos- tril– lip	Nos- tril– eye	Eye– tym- panum	Pad width	Head length	Head width	Snout– vent	Shank length	Fore- arm	Toe length
Female mean	3.18	3.61	2.19	1.73	13.60	14.24	41.00	19.61	9.84	16.03
Male mean	2.76	2.92	1.65	1.33	11.27	11.70	33.36	16.17	8.03	13.04
Standard deviation	0.22	0.21	0.20	0.14	0.67	0.85	1.71	1.13	0.69	1.00
Direction cosines First axis	0.335	0.324	0.176	0.180	0.373	0.346	0.322	0.367	0.347	0.318
Second axis	0.077	−0.027	−0.565	−0.728	−0.001	0.104	−0.068	0.106	0.223	0.262
Roots $H(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	6.00	1.10	0.87	0.71	0.43	0.31	0.23	0.17	0.12	0.09
Variance component	5.07	1.14	0.37	0.16	0.11	0.09	0.03	0.02	0.01	0.01
Per cent of total	72.3	16.3	5.3	2.3	1.6	1.3	0.4	0.3	0.1	0.1

crease in size of the cranial cavity accounts for the significant variation in the growth rates of the limbs and body while axes eight and nine indicate increased rates of growth for the cranial cavity.

The correlation matrix for this subspecies shows most measurements to be highly correlated at greater than 0.01 per cent level of significance. Measurements three and four, eye to tympanum and pad width, are responsible for those coefficients which are not highly significant at $P = 0.01$.

REMARKS. The choice of a subspecific title for this variant of *Hyla regilla* was limited to two descriptions of specimens from the cape of Baja California made by Cope (1866, p. 313; 1889, p. 359). Cope designated the former, *Hyla curta* (1866), as a new species of *Hyla* and the latter, *Hyla regilla laticeps* (1889), as a variant of *Hyla regilla*. Examination of the specimens used to make these descriptions reveals no essential differences, even though the cotypes of *Hyla regilla laticeps* are fully grown adult males. The age difference in these specimens may account for Cope's placing them in different taxonomic categories.

RANGE. The lower half of the Baja California peninsula comprises the range of this subspecies. The northern limit appears to be near San Ignacio,

the southern limit is the bounds of the peninsula itself. Most localities yielding animals of this subspecies were concentrated south of La Paz.

MATERIAL EXAMINED. (402): San Ignacio, Baja California: USMVZ 73355-73363, 73365-73367. El Triumpho, Baja California: CAS 91471-91472. Sierra Laguna, Baja California: CAS 47255-47256. La Trinchera, Baja California: CAS 91059-91071. San Ignacio, Baja California: CAS 90343-90351, 90912-90927. Boca de la Sierra, Baja California: CAS 91462. La Purissima, Baja California: CAS 91277. Puerto Escondido, Baja California: CAS 53662-53669. La Laguna, Baja California: CAS 87892-87895. Palmarito, Baja California: CAS 101162-101201; SDNHM 53960-54077. Los Marteles, Baja California: SDNHM 54078. Todos Santos, Baja California: SDNHM 54079-54086. San Ignacio, Baja California: SDNHM 54177-54191. Las Parras, Baja California: SDNHM 54879-54914. San Jose Comondu, Baja California: SDNHM 55016-55037. Comondu, Baja California: SDNHM 55038-55105. La Laguna, Baja California: SDNHM 55106-55142. Las Lagunas, Baja California: SDNHM 55143-55149.

Hyla regilla hypochondriaca Hallowell, new combination.

Hyla scapularis var. *hypochondriaca* Hallowell, 1854. Cotypes (8): 3235 United States National Museum. Tejon Pass, California, collected by Dr. A. L. Heerman.

COTYPES (8). USNM 3235. Two small adult males, two adult females, four very small juveniles.

PARATYPES. None in existence.

DIAGNOSIS. A moderate to small-sized subspecies of the *Hyla regilla* complex, attaining an average size of 33.5 mm. head–body length; dorsal skin smooth, head wide, tympanum diameter less than one-half the diameter of eye; no vestige of web present between fingers; granulation not visible on breast fold; small nuptial callosity at the base of the first finger; toes one-half webbed; tibiotarsal articulation to anterior edge of eye or beyond.

DESCRIPTION OF THE MALE COTYPES (2). The following measurements were made on the larger of the two male cotypes: Nostril to lip, 2.0 mm.; nostril to anterior edge of eye, 2.4 mm.; posterior edge of eye to anterior edge of tympanum, 1.3 mm.; width of pad on third digit, 0.9 mm.; length of head, 9.3 mm.; width of head, 10.0 mm.; snout–vent length, 26.9 mm.; tibia, 13.0 mm.; forearm length, 6.1 mm.; toe length, 10.4 mm. Head wide at the angle of the jaw rounding quickly forward to form a blunt snout; snout appears squared off in the lateral profile but extends slightly beyond the mouth; eyes prominent, protruding beyond jaw; nostrils prominent surrounded by raised tissue, nostril closer to median anterior edge of upper lip than to the eye; tympanum moderate in size being less than one-half the diameter of the eye; line between the eye and nostril slightly concave.

Vomerine teeth small, lying completely between the choanae, being closer

to each other than to the choanae; choanae easily larger than one tooth group; tongue generally circular in shape, free posteriorly for about two-fifths of its length; vocal sac medial, single, evident on chin by ample folding of skin.

The supratympanic fold very light but visible from the posterior edge of the eye to the insertion of the forearm. The skin above smooth, minutely pustulate becoming granular at the sides, entire abdomen granular, thigh and arm with patches of fine granulation; granulation continues until the breast fold on which it is absent; minute granules are present on the distended membranes of the throat; skin granular in anal region.

Fingers moderate in size, no vestige of web visible, small amount of dermal thickening on the edges of the digits extending to the disks; disks circular in shape, the largest being easily greater than one-half the diameter of the tympanum; small nuptial callosity on the base of the first finger; all remaining fingers and palm with a few tubercles. The foot only moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe extends about halfway up the tibia; both the inner and outer metatarsal tubercles are small, the former located well down on the base of the first toe; remainder of the foot and toes dotted with small tubercles. Toes about one-half webbed with a minute amount of dermal thickening of the toes extending beyond the webbing. Tibiotarsal articulation extends to within the eye.

COLOR IN ALCOHOL. The skin above and on the limbs blue–gray (probably a shade of green in life). A dark stripe runs from beyond the nostril through the eye, widens, involves the tympanum, and terminates at the insertion of the forearm. A dark stripe runs around the upper lip bordered by a cream color. Dorsal markings are evident as darker stripes and spots.

VARIATION. The animals used for biometrical analysis (table 11) follow very closely the description of the cotypes above with the following exceptions: the amount of the tongue free posteriorly is less, about one-third; no vestige of web is present between the fingers; tibiotarsal articulation generally extends beyond the eye. These noted exceptions from the cotype appear to be the case throughout the range of this subspecies. The females of this species show the same morphological characters with the exception of size, the female being larger.

FACTOR ANALYSIS OF *Hyla regilla hypochondriaca*. The first factor shows that primary variation in the size of the animal accounts for 65.5 per cent of the variation. Shank length shows a smaller contribution to variation than its corresponding measurements on the first (size component) axis. This can perhaps be explained by consulting table 11 which shows that *Hyla regilla hypochondriaca* has one of the smallest mean shank lengths. Factors two through ten have differing signs for the direction cosines, and, therefore, correspond to a change in shape, specifically in reduced limb size and increased length of the cranial cavity. Factors eight through ten show secondary variation in the size of the limbs and width of the head.

TABLE 11. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 40 adult males of* Hyla regilla hypochondriaca *are listed with the roots* (λ) *of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
	Nos-tril–lip	Nos-tril–eye	Eye–tym-panum	Pad width	Head length	Head width	Snout–vent	Shank length	Fore-arm	Toe length
Measurement										
Female mean	2.96	3.12	1.65	1.61	12.13	12.88	38.92	18.00	9.71	15.75
Male mean	2.50	2.73	1.26	1.14	10.40	11.11	33.49	15.83	7.93	13.22
Standard deviation	0.23	0.23	0.20	0.19	0.73	0.99	2.51	1.92	0.63	1.29
Direction cosines										
First axis	0.321	0.324	0.269	0.198	0.370	0.363	0.363	0.254	0.339	0.317
Second axis	0.027	0.119	−0.212	−0.781	0.026	0.046	0.132	−0.380	0.334	0.232
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	6.55	0.91	0.71	0.59	0.44	0.24	0.22	0.15	0.12	0.08
Variance component	10.30	2.30	0.62	0.25	0.09	0.06	0.03	0.02	0.02	0.01
Per cent of total	75.2	16.8	4.5	1.8	0.7	0.4	0.2	0.1	0.1	0.1

REMARKS. Hallowell (1854) described *Hyla scapularis,* variation *hypochondriaca,* from Tejon Pass, California, from specimens obtained by Dr. A. L. Heerman. Both Yarrow (1882, Bull. of the U. S. Natl. Mus., vol. 24, p. 172) and Test (1898, Proc. U. S. Natl. Mus., vol. 21, p. 490) list USNM number 3255 as the cotype of *Hyla scapularis,* variation *hypochondriaca*. The cotype series consists of two adult males, two adult females, and five juveniles.

RANGE. *Hyla regilla hypochondriaca* has been collected primarily at localities along the coast of California and part of the western coast of Baja California. The northern limit of the subspecies is near Clear Lake, California, and the southern limit is near Rosario in Baja California. The animals are not found in an easterly direction beyond the coast range of mountains.

MATERIAL EXAMINED. (882): Kernville, California: SU 8937-8942. La Grulla, Baja California: SU 12949-12955. Banner, California: SU 20200-20255 (intergrade between *Hyla r. hypochondriaca* and *H. r. sierrae*). Cedros Island, Baja California: CAS 42049-42056, 56276-56352, 59626-59677. San Telmo, Baja California: CAS 57520-57523. El Rosario, Baja California: CAS 90863-90872. Clear Lake, California: SDNHM 53576-53608. Russian River, California: SDNHM 53609-53642. San Luis Obispo, California: SDNHM 53654-53677. Osoflaco, California: SDNHM 53678-53685. Long Beach, California:

CAS 101110-101133. Salinas, California: SDNHM 53758-53764. Healdsburg, California: SDNHM 53765-53769. French Gulch, California: SDNHM 53782-53806 (intergrade between *Hyla r. hypochondriaca, H. r. deserticola, H. r. pacifica,* and *H. r. sierrae*). Crescent, California: SDNHM 53889-53919 (intergrade between *Hyla r. hypochondriaca, H. r. sierrae,* and *H. r. wrightorum*). Boulder, California: SDNHM 54275-54343. Lake Henshaw, California: SDNHM 54373-54417. Lake Arrowhead, California: SDNHM 54418-54441 (intergrade between *Hyla r. hypochondriaca* and *H. r. sierrae*). Mount Helix, California: SDNHM 54442-54477. Fuerte Farms, California: SDNHM 54478-54491. Presidio, California: SDNHM 54492-54501. Lakeside, California: SDNHM 54502-54560. Jacks, California: SDNHM 54561-54602. Guadalupe, Baja California: SDNHM 54603-54611. Santa Monica, California: SDNHM 54612-54614. Rancho Santa Fe, California: SDNHM 54615-54618. Miramar, California: SDNHM 54622-54624. Kearney Mesa, California: SDNHM 54625. College Drain, California: SDNHM 54626-54633. Bass Lake, California: CAS 101134-101161. White Water Canyon, California: SDNHM 54863-54896. Earthquake Valley, California: SDNHM 54915-54947 (intergrade between *Hyla r. hypochondriaca* and *H. r. sierrae*). Scissors Crossing, California: SDNHM 54961-54982 (intergrade between *Hyla r. hypochondriaca* and *H. r. deserticola*). Banner, California: SDNHM 54985-55002. Barkers, California: SDNHM 555003-55011 (intergrade between *Hyla r. hypochondriaca* and *H. r. sierrae*).

Hyla regilla pacifica Jameson, Mackey, and Richmond, new subspecies.

Holotype. Adult male, number 101007, California Academy of Sciences (CAS). One of a series collected February 27, 1957, at Big Creek State Park, 4 miles S. of Waldport, Lincoln County, Oregon; R11W, T133, S2, NW. 25 feet, by James P. Mackey.

Paratypes. Sixty adult males CAS 101008-10103F; AMNH F4466-F4483; CNHM 154671-154688; SDNHM 53514-53529; USNM 157836-15F851; MCZ 51857-51873; collected at the type locality.

Diagnosis. One of the largest of the subspecies of the *Hyla regilla* complex attaining a mean size of 36.5 mm. head–body length; dorsal skin smooth, ventral granulation visible on breast fold; small vestige of web between inner fingers; toes about one-half webbed; head coloration present; tibiotarsal articulation to anterior edge of eye or beyond.

Description of the holotype. Nostril to edge of lip, 3.2 mm.; nostril to anterior edge of eye, 3.2 mm.; posterior edge of eye to anterior edge of tympanum, 1.7 mm.; width of pad on third digit, 2.0 mm.; length of head, 12.4 mm.; width of head, 13.3 mm.; snout–vent length, 38.0 mm.; tibia, 19.2 mm.; length of forearm, 8.9 mm.; length of fourth toe, 18.3 mm.

Head widened at angle of the jaw sloping slowly to form a blunt snout; tip of snout appears flattened in lateral profile, extending almost perpen-

dicularly up from the mouth; the line from the eye to the nostril slightly concave; eyes prominent but not protruding greatly beyond the jaw; nostril about equally distant from the eye and median anterior edge of upper lip; tympanum moderately large about equal to one-half the diameter of the eye.

Vomerine teeth readily visible located wholly between choanae and lying approximately equally spaced from each other and the choanae; choanae about equal in size to two tooth groups; tongue broadly elliptical in shape and free posteriorly for about two-fifths of its length; vocal sac medial, single, evident on the chin by ample folding of skin.

Light to moderate supratympanic fold extending well to insertion of the forearm. The skin above smooth, becoming granular at the sides; entire abdomen and underside of thigh and arm with a small amount of granulation; granulation below continues until the breast fold where it rapidly diminishes as the vocal sac is formed; skin granular in anal region.

Fingers rather elongated; small vestige of web remains between the inner fingers, but the outer finger has almost none remaining; the third and fourth digits of the left hand are short, having been cut in a marking procedure; there is little evidence of dermal thickening on the margins of the digits; disks on the fingers moderate, circular in shape, being a little larger than the toe disks; width of the widest pad is easily greater than one-half the diameter of the tympanum; nuptial callosity can be distinguished on the base of the first finger, the palm is not heavily covered with large tubercles as in some variants; the foot is extremely elongate, the part from the tarsometatarsal articulation to the tip of the longest toe extending three-quarters of the way up the tibia; the inner and outer metatarsal tubercles are moderately small. The inner toe is webbed at the base, the rest smaller than the finger disks; a well-defined tarsal fold is in evidence. The legs are elongate, the tibiotarsal articulation reaching to well within the eye.

COLOR IN ALCOHOL. Above, on limbs and body, blue–gray color (most probably a shade of green in life). A dark line beginning below the nostril runs through the eye, widens, and continues through the tympanum ending at about the insertion of the forearm. A thin dark line runs around the lip and is bordered by a light cream color. All dorsal markings have been obscured by the preservation medium, but pattern data taken shortly after the animals were collected shows them to have both head and body markings similar to other variants of *H. regilla*.

VARIATION. The range of variation present in the male comprising the data for the biometrical analysis of this subspecies is shown in table 12. The male paratypes of this subspecies follow closely the description of the holotype. The only variation noted is in the extent of tibiotarsal articulation; the holotype specimen appears to be atypical for this character, tibiotarsal articulation extending easily beyond the eye in most animals of this variant.

TABLE 12. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 50 adult males of* Hyla regilla pacifica *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nos-tril–lip	Nos-tril–eye	Eye–tym-panum	Pad width	Head length	Head width	Snout–vent	Shank length	Fore-arm	Toe length
Female mean	3.36	3.44	1.89	2.37	13.16	14.42	43.44	21.30	10.48	19.20
Male mean	2.85	2.81	1.41	1.65	11.06	12.04	36.46	18.34	9.00	16.35
Standard deviation	0.30	0.25	0.19	0.31	0.75	0.80	2.73	1.70	0.71	1.70
Direction cosines										
First axis	0.296	0.281	0.228	0.306	0.334	0.332	0.343	0.350	0.331	0.342
Second axis	−0.320	−0.403	−0.572	−0.305	0.144	0.209	0.215	0.107	0.373	0.232
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.23	0.99	0.58	0.39	0.29	0.20	0.10	0.10	0.07	0.05
Variance component	13.75	0.71	0.30	0.17	0.12	0.06	0.05	0.03	0.02	0.01
Per cent of total	90.3	4.7	2.0	1.1	0.8	0.4	0.3	0.2	0.1	0.1

The females of the subspecies show the same characteristics as the males with the exception that the females are generally larger.

FACTOR ANALYSIS OF *Hyla regilla pacifica*. The first axis (table 12) shows the primary variation occurring is the size of the animal. Size variation in *Hyla regilla pacifica* accounts for more than 72 per cent of all variation while change in shape is responsible for the remaining variations. Shank length, snout–vent, and toe length have the largest direction cosines. The signs of all the direction cosines for the first axis are positive, indicating a growth trend or size variation. The remaining factors have a difference in sign indicating shape variation. Factors three through six show the growth of the cranial cavity and enlargement of the limbs. Factors seven to ten exhibit secondary variation primarily in the growth of the limbs.

REMARKS. The subspecific title for this variant was chosen with an eye to geographic location. Since the range of this subspecies is the Washington and Oregon Pacific Coast, the name *Hyla regilla pacifica* was applied. This subspecies has been collected at locations (below) from a southern limit near Cannibal Road, California, to the northern limit near Wenberg, Washington. The subspecies is not found east of the coastal range of mountains.

MATERIAL EXAMINED. (165): Ophir, Oregon: UCMVZ 64538-64545. Tilla-

mook, Oregon: UCMVZ 69538-69588. Alvadore, Oregon: UCMVZ 52421-52426. Reedsport, Oregon: UCMVZ 61751-61755. Cathlamet, Washington: UCMVZ 46430-46433. Wenberg, Washington: SDNHM 53345-53430. Waldport, Oregon: CAS 101008-101037, AMNH 74466-74483, CNHM 154671-154688, SDNHM 53514-53529, USNM 157836-157851, MCZ 51857-51873. Lees Camp, Washington: SDNHM 53562-53575. Cannibal Road, California: SDNHM 53643-53653. French Gulch, California: SDNHM 53782-53806 (intergrade between *Hyla r. pacifica*, *H. r. deserticola*, and *H. r. hypochondriaca*). Greyback, Oregon: SDNHM 55012-55013.

Hyla regilla wrightorum Taylor, new combination.

Hyla eximia wrightorum Taylor (Schmidt, 1953).

Hyla wrightorum Taylor, 1939 Univ. Kansas Sci. Bull., vol. 25, p. 436. Holotype 79141, Museum of Zoology, University of Michigan. Eleven miles south of Springerville, Apache County, Arizona.

HOLOTYPE. Museum of Zoology, University of Michigan 79141. See above.

PARATYPES. USNM 26605-26609, Meadow Valley, Chihuahua, Mexico. USNM 9338 (2 specimens), Santa Fe, New Mexico. UMMZ 79141 (3 specimens), 11 miles south of Springerville, Apache County, Arizona. UMMZ 79143 (4 specimens), David Lee Lake, southwest of Luna, Catron County, New Mexico [8,000 ft.]. UMMZ 79142 (3 specimens), 26 miles north of Luna, Catron County, New Mexico [8,100 ft.]. UMMZ 75734, 1½ miles northwest of Miller's Peak, Huachuca Mountains, Arizona.

DESCRIPTION OF THE HOLOTYPE. An excellent description of this animal is given by Edward H. Taylor (1938). The largest subspecies of the *Hyla regilla* complex, attaining a mean size of 38.47 mm. head–body length; dorsal skin smooth; fine granulation on breast fold and vocal sac; head wide; tympanum diameter greater than diameter of eye; vestige of web between fingers; foot one-third webbed; tibiotarsal articulation to the anterior edge of the eye or beyond; heels distinctly overlap; anterior edge of tibia spotted with brown; no dorsal head markings present.

DESCRIPTION OF THE PARATYPE SERIES. Head widened at the angle of the jaw sloping slowly to give a slightly rounded snout; in lateral profile snout appears blunt, but slightly rounded, extending a short way beyond the mouth; eye moderately prominent, not protruding beyond jaw; the line between the eye and nostril generally straight or very slightly concave; nostril closer to edge of upper lip than to anterior edge of eye.

Vomerine teeth groups large, lying wholly between the choanae; choanae moderate about the size of one tooth group; tongue broadly elliptical, free posteriorly for two-fifths of its length; tongue papillae visible but not prominent; vocal sac medial, single, evident on chin by ample folding of skin.

Skin above smooth, becoming granular on the sides; entire abdomen and

underside of thigh and arm with granules; granulation sparse but visible on breast fold and vocal sac; skin granular in anal region.

A vestige of web present between the fingers; thickened dermal ridge on the edges of the digits extending to the disks; disks on fingers moderate, the width of the widest being equal to or greater than one-half the diameter of the tympanum; nuptial callosity present on the base of the first finger; fingers and palm covered with tubercles of various size; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe reaching one-half the way up the tibia; inner and outer metatarsal tubercles moderate; toes one-third webbed; clearly defined tarsal fold. Tibiotarsal articulation to beyond the eye, when limbs are folded at right angles to body, heels have distinct overlap. A light to moderate supratympanic fold extends from the posterior edge of the eye to the insertion of the forearm.

COLOR IN ALCOHOL. Above, on limbs and body, gray to lavender (probably a shade of green in life). A dark stripe beginning slightly anterior to the nostril runs to the eye, widens, involves the tympanum, continues to low on the sides where it breaks up into irregular patches of coloration. A thin dark line bordered above in cream runs around the upper lip. No dorsal markings are present.

VARIATION. The paratypes and other specimens examined of this subspecies (table 13) follow very closely the description given by Taylor (1938) and the above description of part of the paratype series. Taylor (1938) did not make any mention of the absence of dorsal head markings in his description of the holotype; a photograph (p. 443) shows the holotype to have no visible dorsal head markings. The females of this subspecies show the same characters as the males with the exception that females are generally larger.

FACTOR ANALYSIS OF *Hyla regilla wrightorum*. The direction cosines for the first axis are all positive, indicating a general growth trend or size variation. Those measurements which show general body size have direction cosines of about the same magnitude. Measurements which show the size of the cranial cavity have direction cosines of smaller magnitude corresponding to slower rates of growth. Factors two through four show variation in shape through differences in sign of the direction cosines. Increase in the size of the limbs and cranial cavity are responsible for this variance. The remaining factors show increases in the size of the cranial cavity and the limbs.

RANGE. *Hyla regilla wrightorum* has been collected at locations in Nevada, Arizona, New Mexico, and Mexico. Its range may have been restricted to mountain regions until the advent of men (Funk, 1964; Martin, 1963). The northern limit of collection is near Flagstaff, Arizona; the southern limit near Majarachic, Chihuahua, Mexico.

MATERIAL EXAMINED. (12): Fort Verde, Arizona: AMNH 419. Garden Canon Road, Cochise County, Arizona: AMNH 55073-55074. Alpine, Arizona: AMNH untagged. Majarachic, Chihuahua, Mexico: CNHM 105189-105190.

TABLE 13. *The mean of one adult female and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 10 adult males of* Hyla regilla wrightorum *are listed with the roots* (λ) *of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nos-tril-lip	Nos-tril-eye	Eye-tym-panum	Pad width	Head length	Head width	Snout-vent	Shank length	Fore-arm	Toe length
Female mean	3.20	3.10	1.50	1.40	12.30	13.90	40.20	19.70	9.00	16.70
Male mean	2.98	3.02	1.31	1.46	11.38	12.46	38.47	18.70	8.65	16.11
Standard deviation	0.22	0.23	0.21	0.22	0.65	1.02	3.27	1.24	0.62	1.08
Direction cosines										
First axis	0.344	0.301	0.288	0.208	0.300	0.347	0.333	0.340	0.347	0.329
Second axis	−0.040	−0.398	−0.311	−0.611	0.300	0.225	−0.209	0.278	0.227	0.240
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.39	1.46	0.46	0.32	0.20	0.11	0.06	0.02	0.00	0.00
Variance component	13.73	1.35	0.20	0.08	0.05	0.02	0.01	0.00	0.00	0.00
Per cent of total	88.9	8.7	1.3	0.5	0.3	0.1	0.1	0.0	0.0	0.0

Flagstaff, Arizona: SU 2084 (3). Springerville, Arizona: UMMZ 79141 (2). Luna, New Mexico: UMMZ 79142 (2).

Hyla regilla lafrentzi Mertens and Walterstorff, new combination.

Hyla lafrentzi Mertens and Walterstorff, 1929, Zool. Anz., B. 84, no. 9/10. Type 49/27 Magdeburg Museum. Desierto de los Leones, in mountain forest near Mexico City, Distrito Federal, 3,000 meters, L. Lafrentz, collector, December 18, 1927. Type not now in existence; destroyed during World War II.

NEOTYPE. Natur-Museum Und Forschungs-Institut "Senckenberg" SMF 30997. Collected Desierto de los Leones (3,000 m.), Mexico, by K. Lafrentz, 1927.

PARATYPES. None in existence.

DIAGNOSIS. One of the largest subspecies of the *Hyla regilla* complex, attaining a mean size of 37.71 mm. head–body length; dorsal skin smooth, granulation over entire ventral portion; head wide, vestige of web between first three fingers only, toes one-half to three-quarters webbed; tibiotarsal articulation to beyond eye.

DESCRIPTION OF THE NEOTYPE. Adult male. Nostril to upper edge of lip,

3.0 mm.; nostril to anterior edge of eye, 2.7 mm.; posterior edge of eye to anterior edge of tympanum, 1.2 mm.; width of pad on third finger, 1.4 mm.; length of head, 12.0 mm.; width of head, 13.3 mm.; snout–vent length, 36.9 mm.; tibia, 20.8 mm.; forearm length, 10.0 mm.; length of fourth toe, 16.6 mm.

Head widened at angle of the jaw sloping to give a rounded snout, in lateral profile snout blunt but slightly rounded and extends beyond the mouth; eye moderately prominent protruding slightly beyond the outline of the jaw; tympanum moderate, its diameter being about equal to one-half the diameter of the eye; the line between the eye and the nostril slightly concave.

Vomerine teeth groups moderate lying wholly between the choanae, being slightly closer to each other than to the choanae; choanae about the size of a tooth group; tongue broadly elliptical free posteriorly for about one-third of its length; vocal sac medial, single, evident on chin by folds of skin; sac appears smaller with fewer folds than in some subspecies.

A light supratympanic fold; extends from the posterior edge of the eye to the insertion of the forearm. Skin above smooth becoming granular well down on the sides; entire underside of body including arms, thighs, and vocal sac with granulation.

A vestige of web present between the fingers, slight dermal thickening of the edges of the digits extending to the disks; disks moderate, that of the third finger being the largest, its width easily greater than one-half the diameter of the tympanum; a large nuptial callosity on the base of the first finger; fingers and palm with tubercles of various size; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe reaching one-half of the way up the tibia; inner and outer metatarsal tubercles small, the latter being hardly visible. Toes one-half to three-quarters webbed, the webs continued to the disks as thickened dermal ridges. Tibiotarsal articulation to beyond eye.

Color in alcohol. Above, on limbs and body, blue (probably a shade of green in life). A dark stripe beginning anterior to the nostril runs through the eye, widens, involves the tympanum, and continues well beyond the insertion of the forearm. A thin dark line bordered above in cream runs around the upper lip. Dorsal marking evident as dark spots, two such small spots on the head at the edges of the eyes. Legs and feet spotted; a thin dark line bordered very slightly in cream runs along the anterior edge of the tibia.

Variation. The series of specimens used for biometrical analysis of this subspecies (table 14) follows very closely the above description of the neotype with the following deviation. The eyes do not generally protrude beyond the outline of the jaw; the supratympanic fold is usually well defined, and markings on the head are absent. The females of this subspecies show the same characters as the males with the exception that the female is generally larger.

Factor analysis of *Hyla regilla lafrentzi*. Factor analysis of *Hyla regilla lafrentzi* gave the following results. (See table 14.)

TABLE 14. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 15 adult males of* Hyla regilla lafrentzi *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nostril–lip	Nostril–eye	Eye–tympanum	Pad width	Head length	Head width	Snout–vent	Shank length	Forearm	Toe length
Female mean	3.45	3.43	1.55	1.86	13.82	15.54	45.37	23.80	10.66	20.30
Male mean	3.00	3.05	1.19	1.63	11.82	13.60	37.71	20.29	9.17	16.96
Standard deviation	0.20	0.18	0.25	0.10	0.50	0.81	2.04	0.94	0.58	0.62
Direction cosines										
First axis	0.326	0.273	−0.039	0.244	0.380	0.319	0.375	0.352	0.379	0.322
Second axis	0.112	−0.320	−0.771	−0.197	−0.009	−0.289	0.144	0.124	−0.117	0.345
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	5.90	1.54	0.83	0.62	0.48	0.31	0.19	0.08	0.04	0.01
Variance component	5.73	0.52	0.27	0.12	0.07	0.04	0.02	0.01	0.00	0.00
Per cent of total	84.5	7.7	4.0	1.8	1.0	0.6	0.3	0.2	0.0	0.0

The first axis (table 14) shows that general size variation with the limbs, body, and head account for 59.0 per cent of the primary variation. The direction cosines are all positive for this axis with the exception of a small negative value for measurement of the eye to tympanum. The second factor shows general shape variation in body length and limb size. Axes three through six exhibit general shape variation in both the limbs and head. Factors seven through ten account for the primary variation or growth in the cranial cavity and elongation of the limbs.

The correlation matrix (table 14) for this subspecies gives the correlation coefficients of all different combinations of measurements. The number of coefficients not significant at 0.1 per cent level has reached a peak in this analysis. Eye-to-tympanum and pad width measurements appear to be responsible for the insignificant values. As the first axis of the factor analysis shows both pad width and eye-to-tympanum measurements have the smallest rates of increase of all measurements. The slow rate of growth for these characters accounts for both the negative and insignificant values calculated for the correlation coefficients.

Hyla regilla lafrentzi is characterized as varying primarily in size or growth of the body. Secondary variation is responsible for the elongation of the limbs

and growth of the head and cranial cavity and can be interpreted as shape variation.

REMARKS. The holotype and paratype specimens of *Hyla lafrentzi* (Mertens and Walterstorff), deposited in the Museum of Magdeburg, Berlin, Germany, were destroyed at the end of World War II. Dr. Robert Mertens has asked that we declare the remaining paratype as the neotype of *Hyla lafrentzi* (Mertens and Walterstorff). The neotype (SMF 30997) is deposited in the Natur-Museum Und Forschungs-Institut "Senckenberg," Frankfurt, Germany.

RANGE. The central plateau of Mexico.

MATERIAL EXAMINED (24). Velasco, Hidalgo, Mexico: AMNH 57824-57829. Lagunas de Zempoala, Morelos, Mexico: AMNH 57692-57699. Llano Grande, Mexico, Mexico: CNHM 107182, 107112, 107184, 107297, 107310, 107167, 107189, 107124, 107174.

Hyla regilla palouse Jameson, Mackey, and Richmond, new subspecies.

HOLOTYPE. Adult male, number 100982, California Academy of Sciences (CAS), one of a series collected June 8, 1957, 6 miles SE. of La Grande, Oregon, at the junction of highways US 30 and Oregon 203, 2,800 feet, by Byron E. Lippert.

PARATYPES. CAS 100983-100990, 101345, AMNH 74443-74448, CNHM 154666-154670, USNM 157854-157857, SDNHM 44715-44718, MCZ 51853-51856; collected at the type locality.

DIAGNOSIS. One of the larger subspecies of the *Hyla regilla* complex, attaining a mean size of 34.3 mm. head–body length; dorsal skin pustulate, ventral granulation coarse, heels have a slight overlap; head wide; vestige of web between fingers; toes about one-half webbed; tibiotarsal articulation to the posterior edge of eye.

DESCRIPTION OF THE HOLOTYPE. Nostril to edge of lip, 3.0 mm.; nostril to anterior edge of eye, 3.0 mm.; posterior edge of eye to anterior edge of tympanum, 1.6 mm.; width of pad on third digit, 1.5 mm.; length of head, 11.2 mm.; width of head, 12.2 mm.; snout–vent length, 26.2 mm.; tibia, 26.2 mm.; length of forearm, 8.3 mm.; length of fourth toe, 14.5 mm. Head widened at the angle of the jaw, sloping quickly forward to the nostril and abruptly to the mouth forming a somewhat rounded snout; in lateral profile snout rounded, extending slightly beyond the mouth; eyes moderately prominent, not protruding beyond outline of jaw; nostril a little closer to the edge of lip than to eye; tympanum small, its diameter a little less than that of the eye.

Vomerine teeth small but visible, lying completely between the choanae, with a space of approximately one tooth group between them; choanae a little larger than one tooth group; tongue generally elliptical in shape, free posteriorly for about one-half its length; vocal sac medial, single, evident on chin by ample folding of skin. Moderately heavy supratympanic fold extending to the

insertion of the forearm; skin above pustulate becoming granular at the sides; entire abdomen and underside of arm and thigh granular with remainder of the underside of the legs smooth; granulation becomes smaller on the breast, disappearing in vocal sac; skin granular in anal region. A vestige of web present between the fingers with a thickened dermal ridge extending the length of the digits to the pads; disks distinctly oval in shape, that of the third finger being the largest with a length greater than one-half of the diameter of the tympanum; nuptial callosity present extending from the wrist to slightly beyond the base of the first finger, medial and outer palmar tubercles confluent posteriorly; each finger with many tubercles with exception of the second, which has but one or two; the first and fourth fingers have the largest tubercles situated slightly above the base of the fingers; surface of the palm contains many irregular tubercles which appear to be extensions of the finger tubercles; the second finger of the left hand missing; foot rather elongate, the part from the tarsometatarsal articulation to the tip of the longest toe extends halfway up the tibia; two large metatarsal tubercles are located at the base of the first and fourth toes with the inner tubercle being the largest. Toes somewhat more than one-half webbed, thickened dermal ridges extend to the disks as extensions of webbing; foot and toes contain numerous small tubercles. Tibiotarsal articulation extends to the posterior edge of eye.

COLOR IN ALCOHOL. Upper parts blue–gray with dark dorsal markings; definite eye stripe present, running from the insertion of the forearm, quickly widening to about the diameter of the eye, narrowing at exit from eye, and curving slightly to the nostril where it slopes abruptly and stops approximately one-half the distance down the snout; dark thin stripe runs around the upper lip, edged above in cream color; back of femur is cream yellow with brown reticulation.

VARIATION. The range of variation present in the males providing the data for the biometric analysis of this subspecies is shown in table 15. The 27 male paratypes of this subspecies follow the description of the holotype with the exception that the nostril is generally slightly closer to the edge of the lip. The tongue may be more circular in shape than present in the holotype specimen. The dorsal markings of the paratype series are in most cases generally faded and in some cases appear to be absent. The two female paratypes designated appear small and were probably collected during their first mating season. The females show no dorsal markings, but this is not assumed to be a subspecific characteristic since females from other localities within the range of this variant have obvious dorsal markings similar to the males.

REMARKS. The subspecific name was chosen to correspond to the geographic and ecologic range of this variant which is similar to that of the "Palouse prairie."

FACTOR ANALYSIS. The first factor (table 15) emphasizes that the overall

TABLE 15. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 30 adult males of* Hyla regilla palouse *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nos-tril lip	Nos-tril–eye	Eye–tym-panum	Pad width	Head length	Head width	Snout–vent	Shank length	Fore-arm	Toe length
Female mean	2.77	3.08	1.78	1.68	11.91	13.01	37.13	17.97	8.98	15.17
Male mean	2.80	2.95	1.46	1.49	10.87	12.06	34.26	16.30	8.03	13.68
Standard deviation	0.20	0.19	0.15	0.18	0.72	0.94	2.64	1.55	0.67	1.39
Direction cosines										
First axis	0.303	0.289	0.114	0.313	0.338	0.352	0.349	0.349	0.337	0.345
Second axis	−0.098	−0.023	−0.911	0.134	−0.202	0.120	0.128	0.130	−0.108	0.204
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.46	1.06	0.49	0.36	0.26	0.14	0.10	0.06	0.05	0.04
Variance component	12.43	0.38	0.19	0.10	0.09	0.04	0.02	0.01	0.01	0.01
Per cent of total	93.6	2.9	1.4	0.8	0.7	0.3	0.2	0.1	0.1	0.1

growth of the animal accounts for the largest amount of variation (74.6 per cent) on any subspecies. The greatest relative rate of growth occurs in the following body areas: head width, snout–vent length, shank length, and toe length, closely followed by head length and forearm length. Pad width and head height (represented by a nostril-to-lip measurement) show intermediate to slow rates of growth. Nostril-to-eye and eye-to-tympanum measurements show the slowest rate of growth relative to other measurements.

The second factor for *H. r. palouse* shows the greatest rate of growth in the toe length, pad width, shank length, snout–vent, and head width measurements. Those measurements which indicate the growth of the cranial cavity still show a slow growth rate.

The third factor shows the greatest rate of growth in the forearm, pad width, shank length, and toe length measurements. The remaining measurements exhibit slower rates of growth.

The fourth factor shows a marked increase in the growth rates of the following measurements: pad width, nostril to eye, eye to tympanum. The remainder of the measurements show a greatly decreased rate of growth over other previous factors.

Factors five through ten represent a little more than 6 per cent of the variation.

RANGE. *Hyla regilla palouse* has been collected at locations in eastern Washington and Oregon, southern Idaho, and on the border of west central Montana. Its range is thought, therefore, to be confined to low and middle elevations of the foothills and mountain valleys of the northern Rocky Mountains.

MATERIAL EXAMINED (306). Pullman, Washington: CAS 5997-60000. Boise, Idaho: CAS 41536-41539, 43532, 455527-45538, 64138-64150. Lake Como, Montana: USMVZ 31848-31851. Smith's Ferry, Idaho: CNHM 6933-6938. Anthony Lake, Oregon: SDNHM 44685-44695. La Grande, Oregon: CAS 100983-100990, 101345; AMNH 74443-74448; CNHM 154666-154670; USNM 157854-157857; SDNHM 44715-44718; MCZ 51853-51856.

Hyla regilla cascadae Jameson, Mackey, and Richmond, new subspecies.

HOLOTYPE. Adult male, number 101038, California Academy of Sciences (CAS), one of a series collected June 15, 1957 at Bend, Oregon, Deschutes County, one-half mile south of Bend; R12E, T18, S9NW, 3,750 feet, by Abert Minasco.

PARATYPES. CAS 101039-101067; AMNH 74449-74465; CNHM 154696-154713; SDNHM 44971-44987; USNM 157821-157835; MCZ 51874-51889 collected at the type locality.

DIAGNOSIS. One of the largest subspecies of the *Hyla regilla* complex, attaining an average size of 35 mm. head–body length; dorsal skin pustulate, head wide at the angle of the jaw, well-defined supratympanic fold; vestige of web present between fingers; toes fully webbed.

DESCRIPTION OF THE HOLOTYPE. Nostril to edge of lip, 3.5 mm.; nostril to anterior edge of eye, 3.1 mm.; posterior edge of eye to anterior edge of tympanum, 1.5 mm.; width of pad, third digit, 1.7 mm.; length of head, 12.9 mm.; width of head, 14.5 mm.; snout–vent length, 39.9 mm.; tibia, 19.1 mm.; length of forearm, 1.4 mm.; length of fourth toe, 16.7 mm. Head widened at the angle of the jaw sloping slowly to the eyes, forming a slightly rounded snout; in later profile snout appears rounded, extending only slightly beyond mouth giving the appearance of a slightly blunted snout; eyes prominent but not protruding beyond the outline of the jaw; nostril about the same distance from median anterior edge of upper lip as from the eye; line from the nostril to eye slightly concave; tympanum relatively small, its diameter being less than one-half the diameter of the eye.

Vomerine teeth groups visible lying close together with less than the width of a tooth group between them; choanae about the size of a tooth group; tongue generally circular in shape, free posteriorly for only two-fifths of its length; vocal sac medial, single, evident under chin by ample folding of skin.

A moderately heavy supratympanic fold present extending from slightly posterior to the eye to the insertion of the forearm. The skin above pustulate

becoming granular on the sides; entire abdomen and underside of thigh and arm granular; granulation extends to the breast fold where it begins to diminish but it is still evident until the colored portion of the vocal sac; skin granular in anal region.

An easily perceivable vestige of web is present between the fingers and a thickened dermal ridge extends to the finger disks; disks distinct, elliptical, only slightly wider than the digits, but greater than half the diameter of the tympanum; a large nuptial callosity is found on the base of the first finger, many tubercles both large and small on the palm and fingers; the fourth digit on the right hand is short and appears to have been cut in marking; foot moderate in length, the part from the tarsometatarsal articulation to the tip of the longest toe extending one-half the way up the tibia; inner and outer meta-tarsal tubercles readily evident, foot is dotted with numerous other small tubercles, webbing generally extends the full length of the toes, becoming nar-row at the tips; tibiotarsal articulation extends to the posterior edge of the eye.

COLOR IN ALCOHOL. Above and on limbs a blue–gray color (probably green in life); dorsal markings dark and distinct. A dark stripe beginning slightly beyond the nostril runs to the eye, and widening, involves the tympanum, and becomes discontinuous at the insertion of the forearm continuing in a series of patches down the side of the animal. A dark stripe bordered above in cream runs around the upper lip.

VARIATION. The ranges of variation present in the males comprising the data for the biometric analysis of this subspecies are given in table 16. The male paratypes of the type series follow closely the definition of the holotype. The females designated as paratypes show the same characters as the males except in respect to size, the female being generally larger.

FACTOR ANALYSIS OF *Hyla regilla cascadae*. The first factor emphasizes in-crease in size (73.6 per cent) and shows about equal rates of increase for snout–vent, shank length, head width, nostril to eye, nostril to lip, and fore-arm; somewhat slower growth rates are exhibited by toe length, eye-to-tympanum, and pad width measurements.

The second factor emphasizes primarily the growth of the eye-to-tympanum measurement. Slower rates of increase are indicated by nostril to eye, toe length, shank length, and head length. The remaining measurements show greatly de-creased rates of growth. The first two factors have accounted for 95.17 per cent of all variation present.

Factors three through ten primarily indicate a secondary increase in the growth rates of the foot and cranial regions.

The correlation matrix for this subspecies (table 16) shows high positive correlation between all different combinations of measurements. Since correla-tion coefficients involving measurement three do not result in insignificant values as previously, one must assume that either the tympanum and eye are

TABLE 16. *The mean of 10 adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 46 adult males of* Hyla regilla cascadae *are listed with the roots* (λ) *of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code Measurement	1–NL Nos-tril–lip	2–NE Nos-tril–eye	3–ET Eye–tym-panum	4–PW Pad width	5–HL Head length	6–HW Head width	7–SV Snout–vent	8–SL Shank length	9–FA Fore-arm	10–TL Toe length
Female mean	3.14	3.47	1.86	1.73	13.10	14.42	41.54	20.03	9.90	16.36
Male mean	3.03	2.97	1.55	1.48	11.70	12.78	36.82	17.69	8.62	14.62
Standard deviation	0.35	0.32	0.24	0.25	1.09	1.28	3.36	1.80	0.88	1.84
Direction cosines										
First axis	0.337	0.334	0.267	0.247	0.344	0.343	0.348	0.343	0.329	0.243
Second axis	−0.041	0.199	0.501	−0.736	0.119	0.040	−0.126	0.136	−0.302	0.156
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.36	0.78	0.69	0.43	0.20	0.17	0.15	0.10	0.08	0.05
Variance component	18.19	2.06	0.93	0.21	0.19	0.16	0.03	0.02	0.01	0.00
Per cent of total	83.4	9.5	4.3	1.0	0.9	0.7	0.1	0.1	0.0	0.0

small or the growth of the head and cranial cavity results in a wider separation of the eye and tympanum.

Primary variation in this subspecies occurs in the growth of the body and limbs. The growth of the cranial cavity matches the growth rate of general body size and in the second factor accounts for a very significant amount of variation. The remaining variation is accounted for by the growth of the foot and secondary enlargement of the head and cranial cavity.

RANGE. *Hyla regilla cascadae* is found in the Cascade Mountains of central Oregon, Washington, and southern British Columbia. The subspecies has its northern limit in Vernon, British Columbia; its southern limit is Klamath Falls, Oregon.

MATERIAL EXAMINED (377). Fort Klamath, Oregon: UCMVZ 35105-35125. Okanagan Lake, British Columbia: UCMVZ 24783-24787, 24791. Mitchell, Oregon: UCMVZ 26719, 26720, 26722, 26723. Twin Buttes, Washington: UCMVZ 29132-29135, 29138. Klamath Falls, Oregon: CAS 20428-20473. West Fir, Oregon: CAS 101068-101803, SDNHM 44744-44794. Hand Lake, Oregon: CAS 101084-101103, SDNHM 44815-44836. Madras, Oregon: SDNHM 44837-44842. East Lake, Oregon: CAS 101104-101115, SDNHM 44843-44848, 44860-44898. Horse Lake, Oregon: SDNHM 44899-44907. Bend, Oregon:

CAS 101038-101067, AMNH 74449-74465, CNHM 154696-154713, SDNHM 44971-44987, USNM 157821-157835, MCZ 51874-51889.

Hyla regilla sierra, new subspecies.

HOLOTYPE. Adult male, number 100991, California Academy of Sciences (CAS), one of a series collected June 26, 1964, 1¼ miles SSE. of Tioga Pass Ranger Station (east of entrance to Yosemite National Park); R25E, T1N, S31, 9,600 feet, by Timothy A. Lyerla.

PARATYPES. CAS 100992-101006, AMNH 74484-74490, CNHM 154689-154695, SDNHM 53835-53841, USNM 157858-157864, MCZ 51890-51896; collected at the type locality.

DIAGNOSIS. One of the largest subspecies of the *Hyla regilla* complex, attaining an average size of 36.4 mm. head–body measurement; dorsal skin smooth; head wide at jaw angle, tympanum greater than or about equal to one-half the diameter of eye; vestige of hand web present; toes one-half to three-quarters webbed; tibiotarsal articulation to the anterior edge of the eye or beyond.

DESCRIPTION OF THE HOLOTYPE. Nostril to edge of lip, 3.5 mm.; nostril to anterior edge of eye, 3.4 mm.; posterior edge of eye to anterior edge of tympanum, 1.5 mm.; width of pad, third digit, 1.9 mm.; length of head, 13.6 mm.; width of head, 14.5 mm.; snout–vent length, 38.2 mm.; length of forearm, 9.5 mm.; length of fourth toe, 16.0 mm. Head widened at the angle of the jaw sloping slowly to the eyes, then more quickly to give a slightly rounded snout; in lateral profile snout appears blunt but extends slightly beyond the mouth; eyes prominent but do not protrude beyond jaw; nostrils prominent, being closer to the edge of the upper lip than to the eye; the line between the eye and the tympanum concave; tympanum moderate in size being equal to or greater than one-half the diameter of the eye.

Vomerine teeth groups moderate in size, lying completely between the choanae; teeth groups are closer to each other than to the choanae; choanae larger than a tooth group, possibly as large as two, tongue large, generally circular in shape; tongue papillae easily seen; tongue free posteriorly for about one-third of its length; vocal sac medial, single, evident in the chin by ample folding of skin, its elongate openings lying lateral to the posterior part of the tongue. A heavy supratympanic fold is evident extending from the posterior edge of the eye to the insertion of the forearm.

The skin above is essentially smooth becoming finely granular at the sides; entire abdomen with moderate-sized granules; undersides of the femurs and arms are spotted with fine granules; the skin of the breast fold smooth; fine granulation continues well into the vocal sac; skin granular in anal region.

Fingers moderately elongate with a vestige of web remaining; average dermal thickening of the edges of the digits is seen; finger disks larger than one-half the diameter of tympanum; rather large nuptial callosity on the base

of the first finger; remainder of the fingers covered with various sizes of
tubercles; three large outer tubercles on palm; foot elongate, the part from
the tarsometatarsal articulation reaching one-half of the way up the tibia;
inner and outer metatarsal tubercles easily seen and are moderately large, toes
with several large tubercles, the foot with only a few small ones. Toes one-
half to three-quarters webbed with obvious dermal thickening of toe disks;
toe disks much smaller than the finger disks and former are not much broader
than width of the toes. Tibiotarsal articulation extends beyond the eye but
not the nostril.

COLOR IN ALCOHOL. Above and on limbs a light blue–gray (a shade of gray
to green in life); dorsal markings, dark, distinct. A dark eye stripe beginning
slightly below the nostrils running through the eye, widening, involves the
tympanum, becomes discontinuous at the insertion of the forearm, and con-
tinues down the side as patches of coloration. The animal lacks a dark line
above the upper lip.

VARIATION. The ranges of variation present in the animals comprising the
data for the biometrical analysis of this subspecies are shown in table 17.
The females of this subspecies are generally similar to males but larger in size.
Color variation in this subspecies is low but present, with gray being the
dominant hue seen. Red, green, and brown animals have been collected, however.

FACTOR ANALYSIS OF *Hyla regilla sierrae*. The direction cosines for the first
axis (table 17) indicate relatively equal rates of growth for shank length, head
length, snout–vent, head width, and nostril to eye; toe length, forearm, and
nostril to lip exhibit intermediate growth rates, and eye-to-tympanum and pad
width show the slowest rates of growth. Again the direction cosines are all
positive, indicating the primary size variation or a growth trend of 70.5 per
cent.

The second factor shows the greatest rate of growth in the forearm and
toe length measurements. Snout–vent, shank length, and head width exhibit
intermediate rates of growth. The direction cosines for this and the remaining
axes differ in sign, indicating a shape variation.

Factors four, five, and six show shape variation to be occurring primarily
in those measurements showing the size of the cranial cavity.

Factors seven through ten show secondary variation in growth of body size,
the limbs, and the head. The correlation matrix for this subspecies shows a
high positive correlation for all different combinations of measurements. *Hyla
regilla sierrae* shows variation similar to the other subspecies of this group.
The greatest amount of variation is accounted for by a growth trend or change
in size; the remaining variation indicates a change in shape. Enlargement of
the cranial cavity is responsible only for secondary variation.

RANGE. *Hyla regilla sierrae* is found in the mountains of the Sierra Nevada
range primarily at high elevations and has not moved extensively in an east–west
direction. The northern limit is the Pine Forest Mountains of northwestern

TABLE 17. *The mean of nine adult females and the mean, standard deviation, and direction cosines of the first and second principal component axes of 10 measurements of 39 adult males of* Hyla regilla sierrae *are listed with the roots (λ) of the correlation matrix and the roots and per cent of total of the variance–covariance matrix. Complete listings of the direction cosine matrix and correlation matrix can be obtained from the authors.*

Measurement number and code	1–NL	2–NE	3–ET	4–PW	5–HL	6–HW	7–SV	8–SL	9–FA	10–TL
Measurement	Nos-tril-lip	Nos-tril-eye	Eye-tym-panum	Pad width	Head length	Head width	Snout-vent	Shank length	Fore-arm	Toe length
Female mean	2.88	3.40	1.39	1.56	12.98	14.44	40.41	20.18	9.82	16.10
Male mean	2.74	2.98	1.37	1.36	11.22	12.46	35.23	17.37	8.63	14.07
Standard deviation	0.30	0.26	0.25	0.43	0.91	1.20	2.93	1.77	0.84	1.42
Direction cosines										
First axis	0.311	0.332	0.237	0.230	0.351	0.340	0.342	0.357	0.315	0.319
Second axis	−0.239	−0.005	−0.523	−0.606	−0.082	0.133	0.190	0.126	0.351	0.320
Roots $W(\lambda)$	1	2	3	4	5	6	7	8	9	10
Correlation matrix	7.28	1.17	0.54	0.25	0.22	0.20	0.14	0.09	0.08	0.05
Variance component	15.41	0.74	0.41	0.19	0.16	0.12	0.06	0.03	0.02	0.01
Per cent of total	89.9	4.3	2.4	1.1	0.9	0.7	0.4	0.2	0.1	0.1

Nevada and its southern limit is Lake Gorman, California. More southerly populations exist (Lake Arrowhead, California; Julian, California) but the animals show intergradation with *H. r. hypochondriaca* and *H. r. deserticola.*

MATERIAL EXAMINED (531). Paradise Valley, Nevada: UCMVZ 1256, 1258, 1570, 1572, 1574. Flanigan, Nevada: UCMVZ 21404-21406, 21409-21410, 21414, 21417, 21419, 35006-35009. Incline, Nevada: UCMVZ 14619-14642. Strawberry Lake, California: SU 7294, 7296-7311. Saratoga Hot Springs, California: SU 13074-13081 (intergrade between *Hyla r. sierrae* and *H. r. deserticola*). Afton Station, California: SU 9413-9416 (intergrade between *Hyla r. sierrae* and *H. r. deserticola*). Banner, California: SU 20200-20225 (intergrade between *Hyla r. sierrae* and *H. r. hypochondriaca*). Yosemite, California: CAS 100991-101006, AMNH 74484-74490, CNHM 154689-154695, SDNHM 53835-53841, USNM 157859-157864, MCZ 51890-51896. Lake Van Norden, California: SDNHM 53870-53888. Crescent, California: SDNHM 53889-53919. Julian, California: SDNHM 54192-54274. Lake Gorman, California: SDNHM 54344-54372. Lake Arrowhead, California: SDNHM 54418-54441 (intergrade between *Hyla r. sierrae* and *H. r. hypochondriaca*). East end of Lake Van Norden, California: CAS 101278-101317. Willows, California: CAS 101202-101277. Earthquake Valley, California: SDNHM

54915-54947 (intergrade between *Hyla r. sierrae* and *H. r. hypochondriaca*).
Barkers, California: SDNHM 55043-55011 (intergrade between *Hyla r. sierrae*
and *H. r. hypochondriaca*). Doerfler, California: SDNHM 55014-55015.

Morphological Comparison of the Subspecies of *Hyla regilla*

The subspecies of *Hyla regilla* appear to fall into three divisions on the
basis of similar morphological characters. These groups are: *Hyla regilla regilla,
H. r. deserticola, H. r. curta, H. r. hypochondriaca*, "thermal forms"; *Hyla
regilla pacifica, H. r. wrightorum, H. r. lafrentzi*, "pluvial forms"; and *Hyla
regilla palouse, H. r. cascadae*, and *H. r. sierrae*, "mountain forms."

Separation of *Hyla regilla regilla* from *Hyla regilla deserticola* is accom-
plished in the following way: *H. r. deserticola*—tongue one-half free posteriorly,
H. r. regilla—tongue two-fifths free posteriorly; *H. r. deserticola*—no vestige of
hand webbing, *H. r. regilla*—shows vestige of hand webbing; *H. r. deserticola*—
ventral granulation extends into vocal sac, *H. r. regilla*—ventral granulation does
not extend into vocal sac.

Hyla regilla regilla can be distinguished from *Hyla regilla curta* as follows:
H. r. curta—usually shows greater amount of toe webbing than *H. r. regilla;
H. r. curta*—no vestige of hand webbing, *H. r. regilla*—vestige of hand web
present; *H. r. regilla*—dorsal skin generally smooth, *H. r. curta*—dorsal skin
pustulate; *H. r. regilla*—ventral granulation does not extend into vocal sac,
H. r. curta—scattered ventral granulation into vocal sac.

Separation of *Hyla regilla regilla* from *Hyla regilla hypochondriaca* is ac-
complished in the following way: *H. r. regilla*—nostril equally distant from edge
of upper lip and anterior edge of eye, *H. r. hypochondriaca*—nostril closer to
edge of upper lip than to anterior edge of eye; *H. r. regilla*—skin above
pustulate, *H. r. hypochondriaca*—skin above smooth; *H. r. regilla*—nuptial
callosity on the base of the first finger large, *H. r. hypochondriaca*—nuptial
callosity on the base of the first finger small; *H. r. regilla*—toes three-quarters
webbed, *H. r. hypochondriaca*—toes one-half webbed; *H. r. regilla*—tibiotarsal
articulation to posterior edge of eye, *H. r. hypochondriaca*—tibiotarsal articula-
tion to within or beyond eye.

Hyla regilla deserticola can be separated from *Hyla regilla curta* in the
following way: *H. r. curta*—nostril generally closer to edge of lip than eye,
H. r. deserticola—nostril about equally distant from anterior edge of eye and
edge of upper lip; *H. r. deserticola*—tongue free posteriorly for about one-half
of its length, *H. r. curta*—tongue free posteriorly for about one-third of its
length; *H. r. deserticola*—dorsal skin pustulate, *H. r. curta*—dorsal skin smooth;
H. r. curta generally shows greater amount of toe webbing than *H. r. deserticola*.

Hyla regilla deserticola can be distinguished from *Hyla regilla hypochon-
driaca* as follows: *H. r. deserticola*—nostril equally distant from edge of upper
lip and anterior edge of eye, *H. r. hypochondriaca*—nostril closer to edge of
upper lip than to anterior edge of eye; *H. r. deserticola*—tongue free posteriorly

for one-half of its length, *H. r. hypochondriaca*—tongue free posteriorly for two-fifths of its length; *H. r. deserticola*—nuptial callosity on the base of the first finger moderately small, *H. r. hypochondriaca*—nuptial callosity on the base of the first finger small; *H. r. deserticola*—toes three-quarters webbed, *H. r. hypochondriaca*—toes one-half webbed; *H. r. deserticola*—tibiotarsal articulation to posterior edge of eye, *H. r. hypochondriaca*—tibiotarsal articulation to within or beyond eye.

Separation of *Hyla regilla curta* from *Hyla regilla hypochondriaca* is accomplished in the following way: *H. r. curta*—nuptial callosity on the base of the first finger large, *H. r. hypochondriaca*—nuptial callosity on the base of the first finger small; *H. r. curta*—toes three-quarters to fully webbed, *H. r. hypochondriaca*—toes one-half webbed; *H. r. curta*—tibiotarsal articulation to posterior edge of eye, *H. r. hypochondriaca*—tibiotarsal articulation to within or beyond eye.

The tibiotarsal articulation of the pluvial forms of *Hyla regilla* extend beyond the eye. *Hyla regilla pacifica* can be distinguished from *Hyla regilla wrightorum* in the following manner: *H. r. pacifica*—tympanum size greater than one-half the diameter of the eye, *H. r. wrightorum*—tympanum size less than one-half the diameter of the eye; vomerine teeth groups generally larger in *H. r. wrightorum; H. r. pacifica*—granulation not visible on vocal sac; *H. r. wrightorum*—granulation over entire vocal sac; *H. r. pacifica* generally has a lesser amount of finger webbing; *H. r. wrightorum* has a lesser amount of toe webbing than *H. r. pacifica.*

Hyla regilla lafrentzi and *Hyla regilla pacifica* can be differentiated in the following manner: *H. r. lafrentzi* shows larger vomerine teeth groups; *H. r. lafrentzi* has granulation over the entire vocal sac, *H. r. pacifica* has little or no granulation on the vocal sac; *H. r. pacifica* exhibits finger pads which are less than or equal to one-half the diameter of the tympanum, *H. r. lafrentzi* has finger pads which are easily greater than one-half the diameter of the tympanum; *H. r. pacifica* shows distant dorsal head markings whereas such marking is absent in *H. r. lafrentzi.*

Hyla regilla wrightorum can be separated from *Hyla regilla lafrentzi* by a comparison of these characters: nostril closer to edge of upper lip in *H. r. wrightorum,* nostril closer to anterior edge of eye in *H. r. lafrentzi;* tympanum is less than one-half the diameter of the eye in *H. r. wrightorum,* tympanum greater than one-half the diameter of the eye for *H. r. lafrentzi; H. r. wrightorum* generally exhibits greater choanae size than *H. r. lafrentzi; H. r. lafrentzi* has a greater amount of toe webbing than *H. r. wrightorum.*

The mountain forms of *Hyla regilla* have a vestige of finger webbing, the nostril generally closer to (equal for *H. r. sierrae*) upper lip than to the eye, and the tibiotarsal articulation generally to anterior edge of eye or into eye for *H. r. sierrae.*

Separation of *Hyla regilla palouse* from *Hyla regilla sierrae* is accomplished

by observing that *H. r. palouse* exhibits a rounded snout in contrast to the blunt snout of the *H. r. sierra*. The larger tympanum size, more toe webbing, and longer tibiotarsal articulation separate *H. r. sierrae* from *H. r. palouse*.

Hyla regilla cascadae can be separated from *Hyla regilla palouse* by comparing ventral granulation, finer in *H. r. cascadae*; amount of heel overlap, greater in *H. r. palouse;* kind of supratympanic fold, heavier in *H. r. cascadae;* overall size of the animal; *H. r. cascadae* usually larger.

Hyla regilla cascadae can be distinguished from *Hyla regilla sierrae* by comparing the following characters: relative position of nostril closer to lip in *H. r. sierrae*, equally distant from lip and eye in *H. r. cascadae*; tympanum size, *H. r. sierrae* larger; size of choanae, larger in *H. r. sierrae*; skin texture, slightly pustulate in *H. r. cascadae,* smooth in *H. r. sierrae*; amount of ventral granulation, present in vocal sac for *H. r. sierrae*, not for *H. r. cascadae*; toe webbing, *H. r. cascadae* fully webbed, *H. r. sierrae* less; tibiotarsal articulation, beyond eye in *H. r. sierrae* only, to anterior edge of eye in *H. r. cascadae*.

KEY TO THE SUBSPECIES OF *HYLA REGILLA*

1a. Dorsal skin smooth or minutely corrugate 5
1b. Dorsal skin pustulate 2
2a. (1) Ventral granulation very fine; tongue smaller, less free posteriorly; no vestige of web between fingers .... *Hyla regilla deserticola*
2b. (2) Ventral granulation coarse; tongue larger, more free posteriorly; vestige of web between fingers 3
3a. (2) Head narrow, eyes protrude beyond jaw; toes three-quarters webbed; choanae small .... *Hyla regilla regilla*
3b. (2) Head wide, eyes do not protrude beyond jaw; toes one-half to fully webbed; choanae size variable 4
4a. (3) Ventral granulation fine; toes fully webbed; heels with slight overlap; heavier supratympanic fold; generally a larger animal .... *Hyla regilla cascadae*
4b. (3) Ventral granulation coarse; toes one-half webbed; heels easily overlap; light supratympanic fold; generally a smaller animal .... *Hyla regilla palouse*
5a. (1) Tibiotarsal articulation to posterior edge of eye or less; head narrow, eyes protrude beyond jaw; no vestige of web between fingers .... *Hyla regilla curta*
5b. (1) Tibiotarsal articulation to well within or beyond eye; head width variable, eyes may or may not protrude beyond jaw; vestige of hand webbing may or may not be present 6
6a. (5) Head markings present 7
6b. (5) Head markings absent 9
7a. (6) Vestige of hand web present; tympanum diameter greater than one-half the diameter of the eyes; choanae larger than a vomerine tooth group; head wide, eyes do not protrude beyond jaw; nuptial callosity on base of first finger moderate to large 8
7b. (6) No vestige of hand web present; tympanum less than one-half the diameter of the eye; choanae are small, less than size of a vomerine tooth group; head narrow, eyes protrude beyond jaw; nuptial callosity on base of first finger small .... *Hyla regilla hypochondriaca*

8a. (7) Granulation fine into vocal sac; vestige of web between fingers; toes one-half
to three-quarters webbed; tibiotarsal articulation to within but not beyond eye
_____   Hyla regilla sierrae
8b. (7) Granulation absent in colored portion of vocal sac; small vestige of web between
inner fingers, none present between outer fingers; toes one-half webbed; tibio-
tarsal articulation to beyond eye, may extend to nostril _____   Hyla regilla pacifica
9a. (6) Choanae about the size of a vomerine tooth group; toes one-third webbed; top
of femur, anterior edge of tibia spotted with brown   Hyla regilla wrightorum
9b. (6) Choanae less than the size of a vomerine tooth group; toes one-half to three-
quarters webbed; a dark line bordered above in cream runs down the anterior
edge of the tibia to the foot   Hyla regilla lafrentzi

DISCUSSION

A taxonomic study is essentially a study of the morphology of the animals
being investigated. Studies of the ecology, genetics, and physiology provide
powerful aids to the analysis of the morphological characteristics, but the
critical explanation must involve the presence, absence, or magnitude of this
or that character.

Closely related forms will evolve in the same direction as the result of the
same or similar mutations and the same or similar adaptive requirements, even
when genetic isolation is complete. Some of the populations we are considering
here exchange genes along a large portion of the geographic continuity. Still
others are subject to differences in breeding season, topography, and environ-
mental barriers which seriously limit the gene flow between the populations.
Genetic tests among animals from several of the populations do not appear
to provide the essential clue to the systematic analysis—the animals interbreed
with varying amounts of reduced viability which reinforces our conclusions
concerning the morphological relationships. A premature discussion or summary
of the results of the genetic, developmental, physiological, and ecological
problems involved is not warranted since these studies must be understood in
light of the morphological analysis and of the historical interpretation of this
analysis.

These animals have been faced with a changing, and perhaps what one
could consider a rapidly changing environment, for at least the last dozen
centuries. The glacial, or more properly, pluvial maximum of 11,000 years
ago was followed by an increase in temperature and decrease in surface
moisture terminating in a thermal maximum about 6,000 years ago. The
thermal maximum was followed by a return to less extreme conditions. The
nature of these secular changes is well documented by extensive pollen pro-
files (Hansen, Sears, etc.). The presence of brief periods of extremely warm
or cold cycles superimposed on the general trends is supported by tree ring
analysis and even by available historical records. While tree toads are adapted
to take advantage of available habitats (ponds, trees) in the presence of con-
ditions which are limiting to either survival or reproduction, a large portion

of their distribution and abundance must be dependent on the abilities to avoid extremes. The mountain forms live in the mountains in spite of the necessity to hibernate to escape winter, storms, and glacial movements. The desert animals live where they are by adapting to warm summers, limited and sporadic water, and frequent necessity to aestivate. In the face of secular changes in the environment the animal has three choices: (1) evolve, (2) move, (3) become extinct. In western tree toads a great deal of all three has occurred and is occurring. Certainly these amphibians had a wide distribution during the pluvial maximum (fig. 11) and they were undoubtedly distributed from the edge of the continental glaciers south into Mexico. Their southern distribution may be assumed to have been at higher elevations. In the east they must have extended to the Rockies (perhaps beyond, if the relation to *Hyla andersoni* is demonstrated), and in the west they appeared to have inhabited all areas to the Pacific. The environment of the pluvial maximum was wet and cooler than now; more important, it was variable, and this variability leads us to suggest that some differentiation of animals would be expected at that time. Certainly there appears to have been a prevailing westerly flow of air masses and a rain shadow in this area is to be expected even during pluvial periods.

We suggest that the animals were differentiated into the groups recognizable today: (1) *H. r. palouse*, *H. r. sierrae*, and *H. r. cascadae* lived near and reproduced in the melting snow surrounding the glacial borders; (2) *H. r. pacifica*, *H. r. wrightorum*, and *H. r. lafrentzi* were adapted to the wet conditions *H. r. pacifica* occupies today (along the northwest coast and throughout the pluvial lakes and basins and mountains of western North America); (3) *H. r. hypochondriaca* and *H. r. regilla* occupied the coastal regions of California south of the San Francisco region and the rain shadow area of the inland valleys, north to near the glacial borders; (4) *H. r. deserticola* and *H. r. curta* were animals of the interior and lower latitudes, along the coast of Baja California.

Certainly some geographic variation is to be expected within the above four groups, but we suggest that it is reasonable to think of these groups as recognizably different from each other and perhaps not much differentiated within each group.

There is an abundant literature on the location of glacial refuges. Amphibians appear to require refuges from thermal maxima. The distribution of these animals during the thermal maximum is suggested by figure 12. The "mountain group" (*H. r. palouse*, *H. r. sierrae*, and *H. r. cascadae*) used the remains of glaciers just as they do today. The "pluvial group" refuged along the northwest coast (*H. r. pacifica*), in the mountains of western North America (*H. r. wrightorum*), and in the mountains of central Mexico (*H. r. lafrentzi*). The coastal mountains of southern California must have provided refuge for *H. r. hypochondriaca*. We suggest that *H. r. regilla* survived in springs, meander

Hypothetical Distribution
during Pluvial Maxima

sierra-cascade-palouse
    "mountain group"
pacificae-wrightorium-lafrentzi
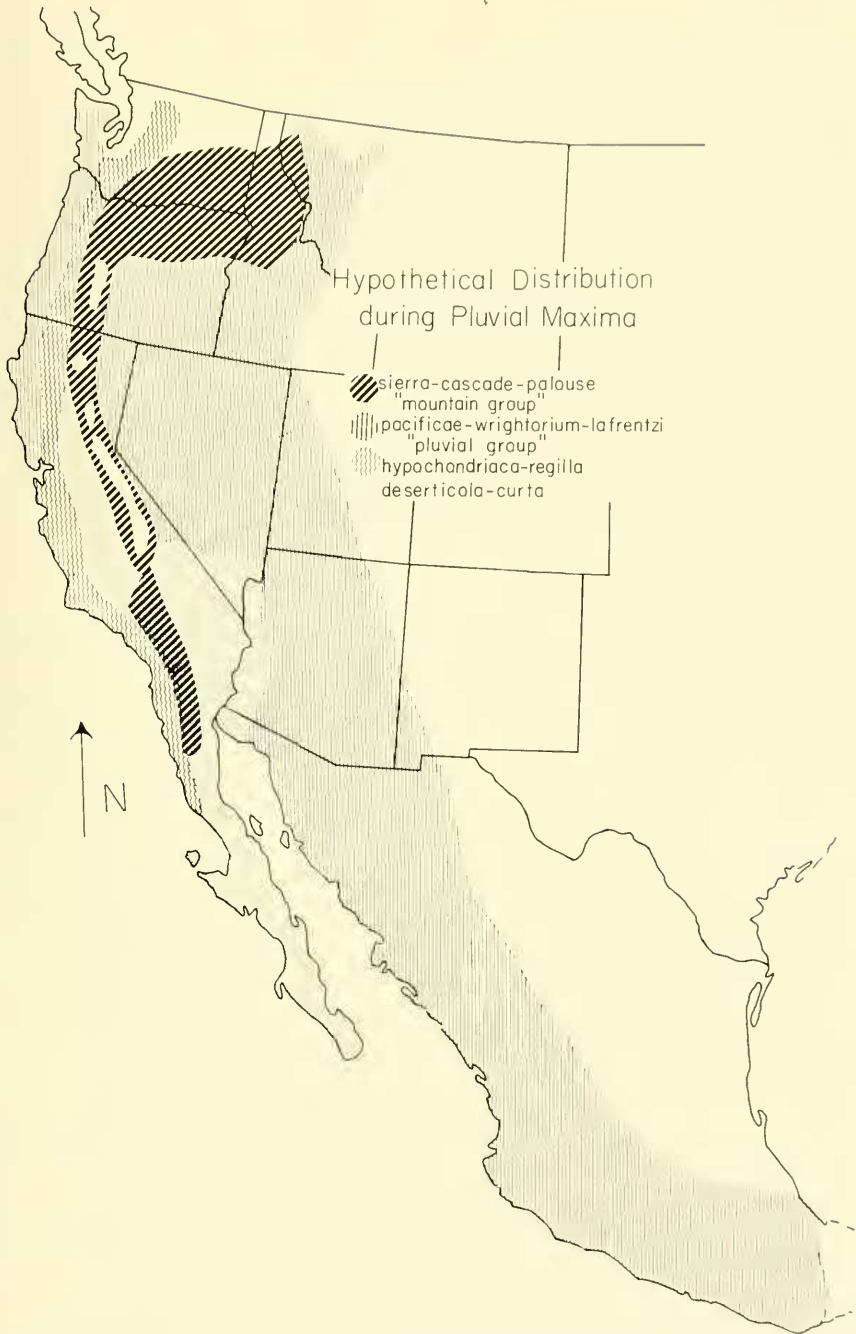   "pluvial group"
hypochandriaca-regilla
deserticola-curta

N

FIGURE 11. Map of the theoretical distribution of the populations of *Hyla regilla* during the pluvial maximum. To the north and within the distribution of the amphibian the white spaces are glaciers. To the east the distribution is unknown.
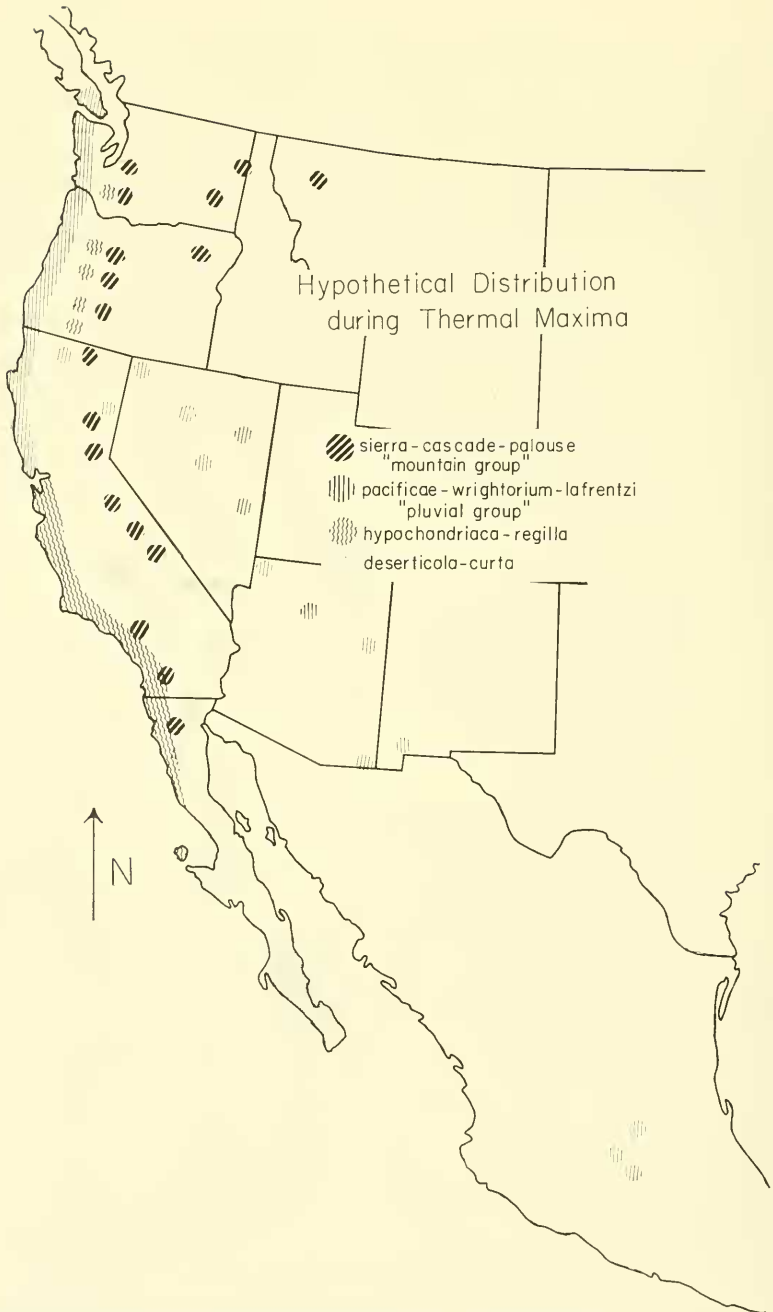
Figure 12. Map of the theoretical distribution of the populations of *Hyla regilla* during the thermal maximum.

scars of rivers, and at least partially at lower elevation west of the volcanic peaks in the area known geologically as the "Old Cascades." The distribution of *H. r. deserticola* during the thermal maximum may be very similar to that of today where it is limited to springs, watering holes, and a few meander scars of the Colorado, San Joaquin, and lower Sacramento rivers. The distribution of *H. r. deserticola* is surely less now than it was four or five hundred years ago when the water table was supported by beaver dams and more extensive vegetation. The mountains of the southern Baja California peninsula provide the logical refuge for *H. r. curta*. The migratory rates are sufficient to explain the range expansions of the animals (fig. 13) following the restrictions of the thermal maximum.

At some point we must come to grips with the problem of phylogenetic relationship in the classic sense (geographic speciation) versus adaptive convergence. This problem was apparent with almost every population we studied and was certainly true of our attempts to group subspecies into related forms. Our data seemed to fit an intermediate position between the accumulation of more and more facts leading in one and only one direction and the position of counting characters to assure repeatable results suggested by some approaches to computer systematics. The counting of characters is not satisfactory for us because of the limited number of things to count and because of the problems of identifying their significance. We are unable to accept the position of complete genetic continuity required by proponents of geographic speciation. We feel that most investigators today are inclined to those portions of all methods available which are useful to explain the results obtained.

Perhaps the most complex problem is that of the relationship within the "pluvial group" of *H. r. wrightorum, H. r. lafrentzi,* and *H. r. pacifica.* The only consistent morphological difference we have been able to find between *H. r. pacifica* and *H. r. lafrentzi–wrightorum* is the absence of head markings in museum specimens of *H. r. lafrentzi* and *H. r. wrightorum,* while almost all other individuals examined have head markings if you examine the specimen carefully. Slight differences in size of vomerine teeth groups, amount of webbing between toes, and amount and kind of coloring can be used in combination to distinguish *H. r. wrightorum* from *H. r. lafrentzi.* From the standpoint of the practicing taxonomist they can be distinguished by their localities. However, a large distance between two localities is not suggestive of adaptive convergence, and nonadaptive convergence of three forms is a little difficult to accept. The relation between *H. r. pacifica* and *H. r. regilla* or *H. r. hypochondriaca* is fully apparent from intergrades and ecological, genetic, and developmental compatibility. The discovery of *H. r. wrightorum* in northern Nevada (at least it was there in 1910) provides further evidence of historical and prehistorical distributions.

If our opinions concerning the influence of the pluvial and thermal maxima on the distribution of these animals is to have meaning, we must consider the

A H. r. palouse
B H. r. cascadae
C H. r. regilla
D H. r. pacifica
E H. r. hypochondriaca
F H. r. sierrae
G H. r. deserticola
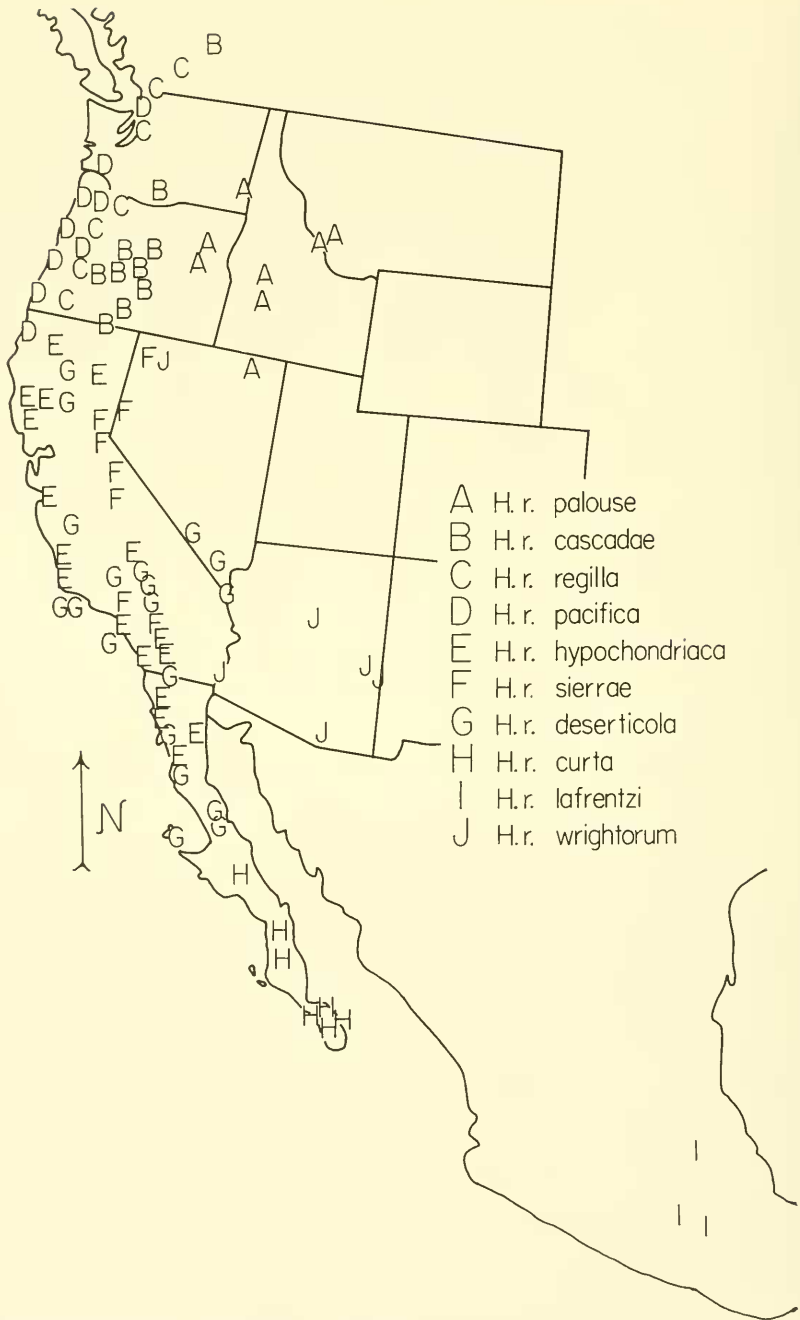H H. r. curta
I H. r. lafrentzi
J H. r. wrightorum

Figure 13. Map of the distribution of the samples used in the statistical analysis. Maps of the detailed distribution of all of the samples studied are not presented.